VOL. XIII APRIL 1959 NO. 2

PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

IN THIS ISSUE: Hurley—*Ecology and Adaptations of Terrestrial Amphipoda* • Banner—*Alpheid Shrimp of the Central Pacific Area* • St. John—*Botanical Novelties on Niihau* • Miller and Pen—*Composition and Nutritive Value of Palolo* • Carlquist—*Vegetative Anatomy of* Dubautia, Argyroxiphium, *and* Wilkesia • Notes

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Notes on the Ecology and Environmental Adaptations of the Terrestrial Amphipoda[1]

D. E. HURLEY[2]

OF THE FEW CRUSTACEAN groups which have achieved some degree of freedom from the marine or freshwater environment, the Amphipoda have received least attention. The terrestrial Talitridae, to which family all of the terrestrial species belong, have been treated in various systematic papers but there is little else. The only nonsystematic work, to my knowledge, is contained in no more than four papers, those of Grimmett (1926), Birch and Clark (1953), Lawrence (1953), and Clark (1955).

Reasons for this neglect are not hard to find. The distribution of the terrestrial species is limited to countries bordering the Indian and Pacific oceans and to the Pacific islands (Fig. 1). In these countries development of zoological studies along other than descriptive lines is relatively recent. It would not be unreasonable to suggest that only South Africa, Australia, and New Zealand have a terrestrial amphipod fauna of sufficient extent and variety to attract attention to their ecology and physiology. And, as Dresel and Moyle (1950) have commented, and I can confirm, the mechanical problems involved in experimental work with the Talitridae are considerable, due in particular to their very great agility and to their susceptibility to dessication. This probably accounts for a general neglect of physiological work, even on littoral amphipods, when compared to the body of research on the closely related Isopoda.

Certainly, the difficulties in collecting terrestrial amphipods are reflected in the two or three species previously described from New Zealand, in contrast to some 40 species or more of terrestrial Isopoda. These difficulties have been overcome to some extent in recent years by modern methods of collecting, and many of the observations made in this paper have resulted from the study of Berlese Funnel material.

Considering the limited systematic work on terrestrial amphipods and the resultant lack of appreciation of their importance in the cryptozoic fauna, one might reasonably expect other research to be somewhat delayed. Nevertheless, there is an open field in Pacific countries for studies on the ecology and physiology of terrestrial amphipods, particularly in relation to soil formation. Such studies, in association with work on other cryptozoic groups, e.g., millipedes and isopods, would be of considerable value in understanding the conversion of leafmould and litter of Pacific forests into highly productive soil.

The abundance of the cryptozoic fauna is often not fully realised. In one particular instance, the animals in a bag of leafmould of less than one cubic foot capacity from Stephens Island, New Zealand, more than half filled a 2-ounce jar, the bulk of weight being made up of a relatively small amphipod, *Orchestia rubroannulata*. Similar large yields of *Talitrus sylvaticus* have been taken under hedges of African boxthorn and other plants in Taranaki, New Zealand.

The abundance of *Talitrus sylvaticus* has also been noted in Australia, where it is widespread in tropical and subtropical rainforests. "In some rain forests near Sydney we have

[1] This paper is, in part, the result of studies carried out at Victoria University College, Wellington, New Zealand, during the tenure of a New Zealand University Research Fund Fellowship. Manuscript received July 8, 1957.

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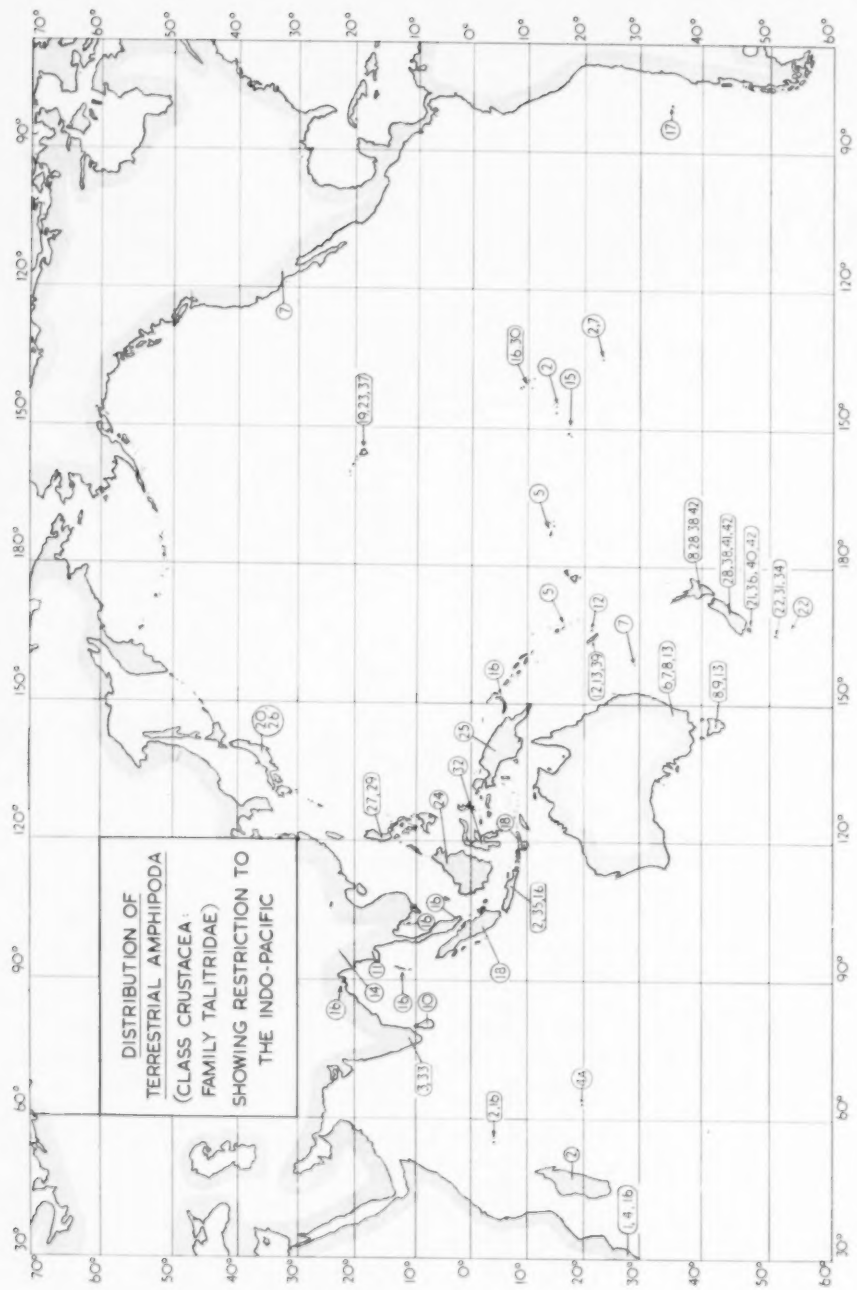
DISTRIBUTION OF
TERRESTRIAL AMPHIPODA
(CLASS CRUSTACEA:
FAMILY TALITRIDAE)
SHOWING RESTRICTION TO
THE INDO-PACIFIC

FIG. 1. Distribution of terrestrial Talitridae. A general map based mainly on the literature to show their restriction to the Indo-Pacific. Misidentifications may contribute to the wide distribution of a few species, e.g., *Orchestia anomala* (16).

The literature references are to papers giving summary and more recent distributional data. This information is not necessarily complete.

1. *Talitrus africanus*	South Africa (K. H. Barnard, 1940).
2. *Talitrus alluaudi*	Seychelles, Madagascar, Java, Tuamotus, Gambier Archipelago, (Stephensen, 1935). Greenhouses and botanical gardens: Belgium, France, Monaco, Switzerland, Germany, Denmark, Hungary, British Isles, Sweden (Shoemaker, 1936; Stephensen, 1935); Czechoslovakia (Cerny and Straskraba, 1957?); U.S.A. (Shoemaker, 1936); U.S.A. and Canada (Medcof, 1939).
3. *Talitrus decoratus*	Nilgiris, India (Carl, 1934).
4. *Talitrus eastwoodae*	South Africa (K. H. Barnard, 1940).
4a. *Talitrus gulliveri*	Annobon Island, Rodriguez Island (Ruffo, 1947).
5. *Talitrus hortulanus*	Samoa, New Hebrides (Stephensen, 1943). Greenhouses: Kew Gardens.
6. *Talitrus kershawi*	Australia (Stephensen, 1935).
7. *Talitrus pacificus*	Australia, Marquesas, Norfolk Island (Hurley, 1955). Botanical gardens: U.S.A. (Shoemaker, 1936).
8. *Talitrus sylvaticus*	Australia, New Zealand (Hurley, 1955); Tasmania (Ruffo, 1948). Botanical gardens: Scilly Isles, Ireland (Hurley, 1955).
9. *Talitrus tasmaniae*	Tasmania (Ruffo, 1948).
10. *Talitrus topitotum*	Ceylon (Burt, 1934).
11. *Talitrus* sp.	Burma (K. H. Barnard, 1935).
12. *Talorchestia antennulata*	New Caledonia, Loyalty Islands (Stephensen, 1935).
13. *Talorchestia diemensis*	Australia, New Caledonia, Tasmania (Stephensen, 1935).
14. *Talorchestia kempi*	Assam (Stephensen, 1935).
15. *Talorchestia rectimana*	Tahiti (Stephensen, 1935).
16. *Orchestia anomala*	Seychelles, Marquesas, ?Andaman Islands, Bismarck Archipelago, Gulf of Siam, Lower Bengal, Singapore, Java, Bali, Westflores, New Britain (Schellenberg, 1938); ?South Africa (K. H. Barnard—*Talorchestia malayensis*, 1955).
17. *Orchestia chiliensis gracilis*	Juan Fernandez (Stephensen, 1935).
18. *Orchestia floresiana*	Flores, Sumatra (Ruffo, 1948).
19. *Orchestia hawaiiensis*	Hawaii (Stephensen, 1935; J. L. Barnard, 1955).
20. *Orchestia humicola*	Japan (Stephensen, 1935).
21. *Orchestia improvisa*	Snares and Stewart islands (Hurley, 1957).
22. *Orchestia insularis*	Campbell and Auckland islands (Hurley, 1957).
23. *Orchestia kaalensis*	Hawaii (J. L. Barnard, 1955).
24. *Orchestia kinabaluensis*	North Borneo (Shoemaker, 1935).
25. *Orchestia* sp. prope *kinabaluensis*	New Guinea (Ruffo, 1948).
26. *Orchestia kokuboi*	Japan (Stephensen, 1935; Bulycheva, 1957).
27. *Orchestia lagunae*	Philippines (Stephensen, 1935).
28. *Orchestia lesliensis*	North and South islands of New Zealand, Stewart Island (Hurle, y1957).
29. *Orchestia luzonensis*	Philippines (Stephensen, 1935).
30. *Orchestia marquesana*	Marquesas (Stephensen, 1935*a*).
31. *Orchestia maynei*	Auckland Islands (Hurley, 1957).
32. *Orchestia montana*	South Celebes (Stephensen, 1935).
33. *Orchestia notabilis*	Cochin State—India (K. H. Barnard, 1935).
34. *Orchestia parva*	Auckland Islands (Hurley, 1957).
35. *Orchestia parvispinosa*	Java (Stephensen, 1935).
36. *Orchestia patersoni*	Snares and Stewart islands (Hurley, 1957).
37. *Orchestia pickeringi*	Hawaii (J. L. Barnard, 1955).
38. *Orchestia rubroannulata*	North Island and Stephens Island of New Zealand (Hurley, 1957).
39. *Orchestia sarasini*	New Caledonia (Stephensen, 1935).
40. *Orchestia simularis*	Snares Island (Hurley, 1957).
41. *Orchestia sinbadensis*	South Island of New Zealand (Hurley, 1957).
42. *Orchestia tenuis*	North and South islands of New Zealand, Stewart Island (Hurley, 1957).

recorded as many as 4000 amphipods per square meter. They are a very conspicuous part of the fauna, both because of their numbers and also because of their habit of jumping when the litter is disturbed. They eat fallen leaves, and there is little doubt that they play a major part in the disintegration of leaf litter in Australian rain forests" (Birch and Clark, 1953).

The observations which follow represent an attempt to piece together information acquired incidentally in systematic studies. They are almost entirely unsupported by experimental evidence, but are tentatively put forward to draw attention to the problems involved and to opportunities for future research.

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I wish to thank Professor L. R. Richardson of the Zoology Department, Victoria University College, Wellington, New Zealand, under whose supervision this work was originally carried out, for his advice and assistance; and also Dr. B. M. Bary and Mr. W. H. Dawbin, who have most generously read the manuscript and offered valuable criticism and encouragement.

DEFINITION

It is necessary to draw attention to past misuse of the term "terrestrial" in speaking of amphipods.

In each of the three talitrid genera, *Talitrus*, *Talorchestia*, and *Orchestia*, there are species of "sandhoppers," amphipods which live in the beach zone above low-tide level and often reach some distance above high-tide mark. These are quite distinct from the terrestrial Amphipoda which inhabit the forest floor of the Indo-Pacific region. In the European zone, where terrestrial species are not indigenous, there has been a tendency to speak of the littoral species as being "terrestrial"; for instance, Dahl (1946) speaks of *Talitrus saltator* as a terrestrial species, one "whose most important functions—eating, breeding, etc. are performed on land." He remarks further that "their main distribution is passive and takes place in sea water." This conclusion points up one of the differences between the truly terrestrial species and those of which Dahl is speaking. The ecology of the terrestrial species is not sufficiently well known to assert in definition that their distribution is active, but it is clear that it does not take place in sea water. Those species of which Dahl speaks should be referred to, I propose, as "supralittoral" (cf., T. A. and Anne Stephenson, 1949). Those species which are essentially independent of sea water, that is, which may occur in leafmould at the water's edge but may equally as well occur in leafmould thousands of feet above sea level and miles away from the seashore, may then properly be referred to as "terrestrial."

The term "cryptozoic" is also used in this paper. It was first proposed by Dendy (1895) for "the assemblage of small terrestrial animals found dwelling in darkness beneath stones, rotten logs, and the bark of trees, and in other similar situations." Interestingly enough, Dendy specifically includes the amphipods, *Orchestia sylvicola*, from New Zealand, and *Talitrus sylvaticus* from Australia, in this fauna.

As an alternative, I have occasionally used the more colloquial term "leafmould species" which is both apt and accurate in describing the niche which these animals fill. It avoids confusion with the supralittoral species, but is of less universal application.

DISTRIBUTION

The most striking feature of the distribution of terrestrial Amphipoda is that they are domiciled essentially in the Indo-Pacific region, and especially in the Southern Hemisphere. Stephenson (1935) no doubt had this localisation in mind when he compiled his paper on "The Indo-Pacific Terrestrial Talitridae," but he did not elaborate any thesis beyond observing that the terrestrial species were characteristic of the Indo-Pacific Ocean,

TABLE 1
GEOGRAPHICAL DISTRIBUTION OF TERRESTRIAL AMPHIPODS
Based on arbitrary geographical regions

SPECIES	REGION																
	Africa–Madagascar	Bay of Bengal	Malay Peninsula	Japan	Philippines	Indonesia–Borneo	New Guinea–Bismarck Arch.	New Hebrides	Loyalty Isles	Australia–Tasmania–Norfolk Is.	New Zealand	Subantarctic Isles	Juan Fernandez	Tuamotu Group	Samoa	Hawaii	U.S.A.
Talitrus africanus	+																
Talitrus alluaudi	+					+								+			+
Talitrus decoratus		+															
Talitrus eastwoodae	+																
Talitrus gulliveri	+																
Talitrus hortulanus								+							+		
Talitrus kershawi										+							
Talitrus pacificus										+				+			
Talitrus sylvaticus										+	+						
Talitrus tasmaniae										+							
Talitrus topitotum		+															
Talitrus sp.		+															
Talorchestia antennulata									+								
Talorchestia diemensis									+	+							
Talorchestia kempi		+															
Talorchestia rectimana														+			
Orchestia anomala	+	+	+			+	+										
Orchestia chiliensis gracilis													+				
Orchestia floresiana						+											
Orchestia hawaiiensis																+	
Orchestia humicola				+													
Orchestia improvisa											+						
Orchestia insularis												+					
Orchestia kaalensis																+	
Orchestia kinabaluensis						+											
Orchestia sp. prope *kinabaluensis*							+										
Orchestia kokuboi				+													
Orchestia lagunae					+												
Orchestia lesliensis											+						
Orchestia luzonensis					+												
Orchestia marquesana														+			
Orchestia maynei												+					
Orchestia montana						+											
Orchestia notabilis		+															
Orchestia parva												+					
Orchestia parvispinosa					+												
Orchestia patersoni											+						
Orchestia pickeringi																+	
Orchestia rubroannulata											+						
Orchestia sarasini									+								
Orchestia simularis											+						
Orchestia sinbadensis											+						
Orchestia tenuis											+						

and that "some species of Talitridae with truly terrestrial habits bear the impression of their terrestrial life." Figure 1, based on available records of distribution in the Pacific area, does not claim to be complete, but does give some idea of the extent of this fauna.

The distribution of species in the Indo-Pacific generally, as at present known, reveals little pattern, due mainly to the fact that most records are of one or two species from each of many island localities.

It is likewise practically impossible to make anything of distributional patterns in Polynesia and Micronesia, but it is interesting to speculate how much of this apparently chaotic distribution, making due allowance for misidentifications, is due to the voyages of the Polynesians. The custom of carrying ample stocks of fern root, taro, yam, gourds, and kumara on long journeys in the very humid and moist atmosphere of their canoes, makes them likely agents of distribution. When more is known of the amphipod distribution pattern, it may be interesting to attempt a reconciliation with ethnological theories of migration and botanical theories of plant distribution by natives in the Pacific.

One might predict an endemic fauna in each island or country where the terrestrial species occur, and where information is available this does seem to be the case. Chilton (1909) recorded five new species of *Orchestia* not found elsewhere from Auckland, Campbell, Snares, and Stewart Island. Stephenson (1938) described *Orchestia patersoni* (as *Talorchestia patersoni*) from Stewart Island. This has since been taken on Snares Island, Bench Island in Foveaux Strait, and Solander Island, all quite close to the original type locality, and there appear to be slight racial differences between some of these localities (Hurley, 1957). The New Zealand fauna includes six described species endemic to the mainland (Hurley, 1957) and at least two further species as yet undescribed, as well as the six species already mentioned from the outlying islands. Of these, only *Talitrus sylvaticus* is known to occur elsewhere. If evidence can be produced to show that the Australian form of *T. sylvaticus* has not been introduced there in the last 200 years from New Zealand, then perhaps the solution to its distribution is to be looked for in the geological history of the two countries. It has been suggested that a New Zealand land mass was connected to Australia and farther north as late as Mid-Cretaceous time but probably not later, and had good connections much earlier which probably extended to take in various northern islands including New Guinea, New Britain, the Solomon Islands, and New Caledonia (Fleming, 1957).

One further possibility is that of transportation by birds, a theory of amphipod distribution for which Segerstrale, *et al.* (1954) has produced considerable geographical and experimental evidence. While there is evidence of considerable migration of bird populations between New Zealand and Australia, it must be said that the distances and the difficulties involved make this theory much less appealing in this instance than, for example, in explaining anomalous discontinuous distribution within New Zealand.

Certain affinities have been suggested in the past between the New Zealand and South African faunas. At present, the terrestrial amphipods of the two countries are considered specifically distinct, and the evidence, in my opinion, suggests parallel evolution from littoral ancestors in the two countries.

There is one surprising fact in this distributional pattern. It is the complete absence of any records from Central and South America, which is especially striking since the forest conditions there are just those which would be expected to support a large fauna of cryptozoic amphipods. Nor do any of the North American records suggest an indigenous fauna. This absence does not seem due to lack of collecting. Allee (1926*a*) in a comprehensive study of leafmould fauna of Barro Colorado Island, Panama Canal Zone, lists no amphipods whatsoever. Other papers I have

noted, including one on the rainforests of Mexico, similarly fail to note their presence. (Allee's paper, surprisingly, also fails to mention Collembola.) Strickland (1945) does not mention amphipods in a study of the soil and litter fauna of forest reserves and cacao estates in Trinidad, British West Indies, although his thorough sampling methods yielded Collembola and Isopoda.[2] The nearest to a South American report is Chilton's description of *Orchestia chiliensis* var. *gracilis* found under stones on Juan Fernandez Island, 590 metres above the sea shore (Chilton, 1920). The shorehopper, *Orchestia chiliensis* s.str., is found on the littoral zone of Juan Fernandez—as well as in Chile and New Zealand.

It is rather less surprising that terrestrial species should be absent from the European continent and the British Isles, especially when the type of forest found there is taken into consideration. It is indicative of this absence that as recently as 1956 a reputable British authority should say: "While the Isopoda have . . . successfully invaded the land, and woodlice lead a completely terrestrial existence, no Amphipoda occur right away from water, although some, like the sandhopper, live around the water's edge. . . . Failure to evolve suitable habits may have prevented the amphipods from becoming truly terrestrial" (Hynes, 1956). (In view of my definition already given of "terrestrial" Amphipoda, it is pertinent to note his reference to occurrence near water.)

Bornebusch (1930), in an extensive survey of the Danish leafmould fauna, failed to record any amphipods whatsoever, although he listed Isopoda, Collembola, Diplopoda, and all other major groups commonly found associated with amphipods in New Zealand leafmoulds. All other accounts of similar collections from the European continent are similarly lacking in amphipods.

The only occurrences on the European continent or in the North American region are those recorded from botanical gardens or greenhouses where they have been accidentally introduced. In every case, the species concerned have since been tracked back to an endemic Pacific origin.

Talitrus alluadi Chevreux was first recorded from the "serres chaudes du Jardin des Plantes de Paris" (Chevreux, 1896). Considered identical with this species are *Orchestia senni*, described by Menzel (1911) from the botanical garden at Basel, and *Talitroides bonnieri* (the name proposed by Stebbing, 1906, for a species described by Bonnier, 1898) found in a conservatory at Ghent. This species, since found endemic in Seychelles, Madagascar, and Archipel de Gambier, Paumotu (Taumotu Islands) and Java, has also been found in greenhouses or botanical gardens in Copenhagen, Cambrai, Grenoble, several cities in Germany, Glasgow, and Norwich (Stephenson, *et al.*, 1924), and in New Jersey and Ohio, U.S.A. (Shoemaker, 1936).

Talitrus hortulanus (Calman, 1912) was described from the Royal Botanical Gardens, Kew, and has since been recorded from Samoa and the New Hebrides (Stephenson, 1943).

Talitrus sylvaticus (Haswell) was recorded as *Talitroides dorrieni* (Hunt, 1925) from Tresco Abbey Gardens in the Scilly Isles. This species, described originally from Australia, has since been found under conditions which suggest that it is endemic to New Zealand. It may also be endemic in Australia or it may have been introduced sufficiently long ago from New Zealand to have achieved a fairly wide distribution and to show minor differences in pleopod armature which possibly warrant subspecific rank (Hurley, 1955).

Talitrus pacificus Hurley, known in the Pacific from Norfolk Island and Australia (Hurley, 1955) and from the Marquesas (Stephenson, 1935, as *T. sylvaticus*) has also been

[2] Since this paper was submitted, Dr. E. L. Bousfield has told me (personal communication) of a "*Talitrator* (sens. Methuen)" from 4,200 feet altitude in Jamaica, B. W. I., and says, "It seems closest to *T. eastwoodae* and may have been introduced, but its wide distribution remote from human habitation and at such altitudes suggests otherwise." I suspect this will prove an exotic species, probably from Africa, associated with plantation introductions. (D. E. H.)

recorded from the United States. Shoemaker (1936) has noted it from Louisiana, and from Balboa Park, San Diego, and Pasadena, California. "*Talitrus pacificus* (is) quite abundant around San Diego. Dr. Johnson used to find dead ones every morning at the east entrance to Ritter Hall. Apparently they had been attracted by the light over the entrance which was left on all night and killed by the insecticide there." (Dr. T. E. Bowman, personal communication.) It is hardly necessary to add that to the Australian or New Zealand visitor to Southern California, the most striking botanical feature there is the widespread cultivation of Australian trees and shrubs.

It has been recognised for many years that there is a considerable "hothouse" fauna. *Placocephalus kewensis* Mosley, a terricolous turbellarian found originally only in greenhouses, and later discovered endemic in a different part of the world, is a good example. Kraepelin (1900) lists a considerable number of introduced animals of different groups found in hothouses in Hamburg, whilst Hatch (1949) discusses Isopoda, Coleoptera, Dermaptera, Orthoptera, and Gasteropoda commonly found in greenhouses of the Pacific Northwest of the United States. Hatch cites the isopod, *Porcellio dilatatus*, as a "properly adapted species which can spread from greenhouse to greenhouse without being able to live in the surrounding situations." In speaking of a "properly adapted species," however, one is overlooking a rather essential feature of this fauna. The fact is that the species is properly adapted for forest floor conditions, but that few situations could be more to the liking of terrestrial amphipods and other cryptozoic fauna than the continuous humidity and the plentiful supply of leafmould for food and cover which most greenhouses provide. If the term "properly adapted" is to be used of anything in this context, it must be applied not to the animals but to the greenhouses.

On this point, Lawrence (1953) makes a most interesting comparison: "The great surface evaporation of the leaves creates a humid mantle around the [South African rain] forest while the foliage of the canopy blankets the substratum from the direct rays of the sun so that it keeps its moisture longer. The atmosphere . . . especially upon a hot day, often recalls that of a greenhouse."

ECOLOGY AND EVOLUTION

The most significant recorded fact in the literature of the terrestrial species is the repeated theme of habitat—"in damp soil in the forests," "among damp fallen leaves," "in burrows in soft damp soil under dead leaves," "on damp earth under logs," "under decaying leaves," and so on. The terrestrial species of amphipods are essentially inhabitants of the leafmould of the forests. They have evolved a habit of life which, while enabling them to colonise a sizable area of the Indo-Pacific land masses, yet imposes very great limitations. Or, bearing in mind the direction from which they have colonised the forests, and that taken by their more advanced relatives, the terrestrial isopods, it would be more correct perhaps to say that the terrestrial amphipods have not yet emerged from the limitations imposed by their cryptozoic environment to any more rigorous habitat.

The change to a terrestrial environment is a major one. There is a complete change of surrounding medium—air is substituted for water. There is a complete change in primary mode of progression, from swimming to jumping, and there is need for modification in most of the important functions of life: breeding, breathing, and excreting. The supralittoral species make the best of both environments. They live within easy reach of the sea, burrowing in wet sand or under stones; they feed on seaweed and animal matter washed up on the shore; they achieve distribution by means of the sea. Many species are able to swim to a certain extent and can survive immersion in sea water (Dahl, 1946).

Carter (1931) considers that the majority of terrestrial animals have reached the land by way of fresh water rather than directly from the sea. "The suggestion is made that this has been partly caused by the favourable series of intermediate environments between the fresh waters and the land, and that the evolution of many of the numerous adaptations necessary for terrestrial life has been induced in these environments serially and therefore with greater ease. The much greater variability of the fresh-water environments has undoubtedly been important in producing this result. The importance of the tide in maintaining the constancy of conditions on the marine littoral is emphasised."

Yet neither amphipods nor isopods fit this general pattern. Among the constituent groups of the cryptozoic fauna Dendy (1895) includes "isolated representatives of typically aquatic groups of animals which have as yet become little modified in accordance with their new life." He comments, "Every naturalist knows how many small animals swarm beneath half-dry stones on the seashore. Such species appear to me to be taking the first step towards a terrestrial life. Gradually, they will make their way inland, still keeping beneath logs and stones for the sake of moisture and coolness, until finally they accustom themselves to a thoroughly terrestrial existence. In this section of the cryptozoic fauna we must place the shrimplike Amphipoda and Isopoda which certainly look strangely out of place on land."

Edney (1954) speaks similarly of the isopods. "There is little doubt that the route to land was across the littoral zone rather than by way of estuaries and swamps (Pearse, 1929). Evidence for this is the existence today of littoral and halophilic forms such as *Ligia* sp. and *Halophiloscia*, which are undoubtedly primitive morphologically."

These views are further supported by the fact that the genera *Talorchestia*, *Talitrus*, and *Orchestia* all embrace supralittoral as well as terrestrial species, whilst the fresh-water species of the family Talitridae all belong to genera which are represented only in fresh water and are morphologically closer to the marine genera of Talitridae than to the supralittoral and terrestrial genera. The constancy of conditions on the marine littoral seems to have barred neither amphipods nor isopods from entering the terrestrial environment.

The forest floor was perhaps the most suitable place for a littoral animal to enter, especially considering that "animals crossing [the littoral] zone may well be subjected to extremely high temperatures" (Edney, 1954). In many lands, the forest reaches right to the water's edge or borders streams running down to the sea, and often beaches are the only barriers between sea and forest. In these places, the supralittoral zone is the beachhead for invasion by littoral species. And, in countries bordering the Pacific where the climate is relatively humid and the conditions of the forest floor are more or less uniform throughout the year, the leafmould zone is relatively moist and stable. Light intensity is considerably reduced by the nature of the zone itself, and by the strata of the forest canopy above. Humidity and temperature are relatively constant. "Forest temperatures are generally lower in summer and higher in winter than temperatures of adjacent areas. Similarly forests are cooler during the heat of the day and warmer during the night than areas external to them. Relative humidity is characteristically higher and evaporation rate lower within the forest than in adjacent, less dense terrestrial communities. Similarly, relative humidity is higher and evaporation rate lower within forests during the night than in daytime" (Allee, Emerson, Park, Park, Schmidt, 1949, references omitted). These tendencies towards a stable and more equable climate are intensified in the leafmould zone which, of its nature, has an insulating effect from the surrounding atmosphere. "The cryptozoa are not only sheltered by the growth of the forest and shrub which mitigates the extremes of light and temperature, but they are further covered

by the damp layer of humus which cuts off all light and movements of air, further reducing the comparatively small fluctuations of temperature and humidity that prevail throughout the forest" (Lawrence, 1953).

The microclimate may change a little but presumably the animals living therein can meet these changes by retreating a little farther and deeper into the leafmould and even into the soil beneath. The annual rhythm of adaptation to climate is then vertical and not horizontal as in the case of, say, the larger vertebrates. For smaller animals, this is an inestimable advantage. In unfavourable conditions their route of escape is not barred by large intractable areas of a biotype in which they cannot survive. In short, they can adjust themselves to seasonal changes without leaving their very specialised niche. When conditions do change abnormally, they may still survive in islands in the forest floor formed, for example, by deep pockets of leafmould, and by fallen and rotting logs which protect the ground beneath. This is well illustrated where forests have been felled or burned off. Under the remnant logs, there is usually a damp area with a relict cryptozoic fauna, absent in the immediately surrounding pasture or scrub. Examination will usually reveal isopods, millipedes, pseudoscorpions, opiliones, centipedes, endemic worms (found very rarely in New Zealand pastures, the pasture species being exotic ones), and, if the area is large and moist enough, amphipods. That land isopods tend to collect in such protected places has been recorded by Allee (1926) who has further shown that isopods will often conserve moisture still longer by aggregating together. This is of positive survival value since aggregated isopods lose moisture more slowly than isolated ones.

In areas of remnant native bush, often the only places where endemic terrestrial isopods are present in any numbers are the ecological islands provided by decaying trees and logs lying on the ground, an effect noted by Dendy (1895) for the cryptozoic fauna generally. "It is far easier to find cryptozoic animals in partially-cleared localities, where they are collected together under the remaining fallen logs, than in virgin forest, where there is so much cover that the animals are widely scattered, and the search becomes very laborious."

On the east coast of the North Island, New Zealand, where there are many such remnants, it is common to find the conglobating and relatively thick-skinned isopod, *Cubaris danae*, in the space between the log and the compact soil below, where there is a little but not a great deal more moisture than in the surrounding unprotected ground. The comparatively thin-skeletoned and nonconglobating *Styloniscus otakensis* is only found in the much moister, rotting wood of the log, associated with ants, peripatus, termites, millipedes, and other invertebrates with similar environmental preferences.

In Australian conditions, Birch and Clark (1953) have noted that amphipods occur in wet years "in the leaf litter of stands of timber in drier habitats such as *Casuarina*, *Eucalyptus*, and *Angophora* forests. But in most years the leaf litter in these forests is too dry for *Talitrus* to survive." However, the fact that repopulation occurs in wet years suggests a survival population in the "drier habitats" or in close proximity.

The fact that no great change in feeding is necessary would facilitate entry to the terrestrial environment. The decaying seaweed diet of supralittoral amphipods is not markedly different from the decaying leaf diet of the terrestrial ones. Birch and Clark (1953) include the amphipod *Talitrus sylvaticus* amongst the litter feeders or "decomposers," commenting that it feeds on leaves only after they have been on the ground for some months.

Terrestrial amphipods, like supralittoral ones, will turn cannibalistic and carnivorous in laboratory conditions when other food is not available, but in normal conditions they seem to be ectophagous rather than predatory. Lawrence (1953) remarks that "the intestine of *Talitrus* (*Talitroides*) *eastwoodae*

living in South African indigenous forests contains only the small fibrous particles of plants and other woody detritus."

Grimmett (1926) attempted to correlate the distribution of male talitrids with the nature of the forests in which they occurred and was led to this statement. "The males of [*Parorchestia sylvicola*] are known to be rather rare. All the specimens collected were therefore determined for sex, the large flattened front legs of the male being, on the suggestion of Dr. Chilton, used as a guide. It was found that in a total of 383 specimens from the beech-forest locality, 43, or 11.2 per cent were males, while in a total of 333 from the tawa forest no males were discovered, though each specimen was carefully examined with a dissecting lens. Moreover, the males in the former were fairly evenly distributed throughout all the samples. It would thus appear that males are extremely rare, or are not produced in the lower-altitude forest during this portion of the year. Temperature, dependent on altitude, is suggested as the environmental factor most likely to be involved."

Unfortunately, there is a simpler explanation which makes his conclusions of little value. Almost certainly he was dealing with two species, one an *Orchestia* with a large well-developed second gnathopod in the male, and the other a species of *Talitrus* with the feebly developed, femalelike second gnathopod in the male which is characteristic of that genus (cf. Fig. 3). It is worth noting that Forster (1954) finds no evidence of altitudinal speciation or correlation between distribution and type of forest cover in the opiliones, and I believe this finding applies equally well to the amphipods.

However, males are often absent from samples—Grimmett's figures suggest a normal proportion of one male in ten—but whether this is due to ecological factors is doubtful. When collecting by hand, there is possibly more chance of favouring one sex, due to such things as size and agility differences between sexes, or the possibility of sexual preferences for different depths in the leafmould. The season of the year, the biology of the species concerned, and location of the sample may affect the percentage of males. There is also no evidence that Grimmett's figures are the norm for all species.

SPECIATION

In spite of our relatively poor knowledge of the cryptozoic amphipods, the number of species already known is surprisingly high and past experience suggests that future work will reveal many more. From the New Zealand region alone, some 14 species are known, and the fauna is by no means intensively studied.

There are two lines of development towards the terrestrial environment, represented by *Talitrus* and *Orchestia* (and perhaps a third by *Talorchestia*). The supralittoral species of these genera form a basically compact group, varying generically only in combinations of gnathopod shape and other comparatively minor morphological variations—minor, that is, compared to generic distinctions in other families. There is, in fact, a tendency for *Talorchestia* and *Orchestia* to intergrade. However, the morphology of the terrestrial species of *Orchestia* and *Talitrus* suggests that they have arisen independently from supralittoral species.

It is also of interest that, whereas littoral species tend to be somewhat cosmopolitan, as may be seen by comparing the faunal lists for New Zealand and South Africa, the terrestrial species are noticeably localised.

It is not difficult to suggest reasons for the proliferation of species. The island nature of the Indo-Pacific provides textbook conditions for speciation due to reproductive isolation. The terrestrial fauna of the subantarctic islands, as recorded by Chilton (1909), suggests speciation through geographical isolation. With some exceptions, the terrestrial species of Polynesia and Melanesia also suggest geographical isolation.

Within New Zealand, Forster (1954) and Dell (1955) have suggested a possible cor-

relation of geographical speciation in leafmould animals with major events in past geological history, including glaciation. According to Forster (1954), the opilionid fauna of Stewart Island "suggests a series of invasions and reinvasions from the mainland following periods of isolation of sufficient time length to permit physiological isolation to be achieved." Further, "the distribution of the fauna of the West Coast of the South Island is strongly suggestive of bio-glacial control, paralleling as it does that of the *Paryphanta* snails for which Willett (1950) postulated a similar origin."

The formation of ecological islands, to which leafmould is particularly susceptible by the presence of such faunal barriers as rivers, mountain ranges, and valleys, also provides a marked stimulus to speciation. This has been noted for other leafmould animals. Speaking of the land molluscs of Fiordland, Dell (1955) comments ". . . such isolated pockets would form ideal localities in which speciation could proceed. The comparatively high number of forms of such a genus as *Ptychodon* could well be due to such a situation, coupled with subsequent invasions."

The mechanism of speciation is perhaps less obvious but I would suggest that the most probable is speciation by neotony—the retention of juvenile or embryonic characters in the adult.

In most species of *Orchestia*, including all of the supralittoral ones, the second gnathopod is large and subchelate in the male, and small and feebly chelate in the female. In *Talitrus* the male second gnathopod is small and feebly chelate, superficially indistinguishable from that of the female. Since the greatly developed male gnathopod in *Orchestia* is known to be used for grasping and even "carrying" the female *in coitu*, there is a strong likelihood that the large size of the male gnathopod is unnecessary in *Talitrus* because of changed sexual habits.

The terrestrial species of *Orchestia*, unlike the supralittoral ones, show gradations in size and type of male gnathopod from the typical *Orchestia* form to a form not far removed from the typical *Talitrus* gnathopod. These "intermediate" species show striking resemblances to the various stages in the development of the male second gnathopod in supralittoral species of Talitridae. A typical series is shown in Figures 2 and 3, where various adult male second gnathopods of "intermediate" forms are contrasted with growth stages of *Talorchestia hottae* (figured by Chilton, 1921, as *T. martensii*). The suspicion that these "intermediate" forms are no more than subadult is, I believe, unwarranted. All other evidence from morphology and distribution points to the animals being genuinely mature.

The other striking morphological feature of the terrestrial species is the trend to reduction of pleopods from the normal supralittoral and marine condition, with three pairs of fully-developed biramous pleopods, to the extreme in *O. patersoni*, a terrestrial species with three pairs of vestigial triangular stumps. The possibility that this trend is also an effect of species formation by neotony has been considered, but limited examination of supralittoral juveniles showed fully formed pleopods at an extremely early stage in development. While it is possible that pleopod formation passes through a bud stage similar to the vestigial stump, it would have to occur at a very early stage and would probably be revealed only by study of the late embryo. Nevertheless, the diagrammatic representation of pleopod structure in Figure 3 indicates that reduction of pleopods and reduction in size of male gnathopods occur more or less in phase and are not inconsistent with the process of neotony.

MORPHOLOGICAL AND PHYSIOLOGICAL ADAPTATIONS

Work on the systematics of the terrestrial amphipods has revealed some interesting tendencies in adaptation. There are no morphological changes of any significance in the mouth parts, but in view of the similarity of

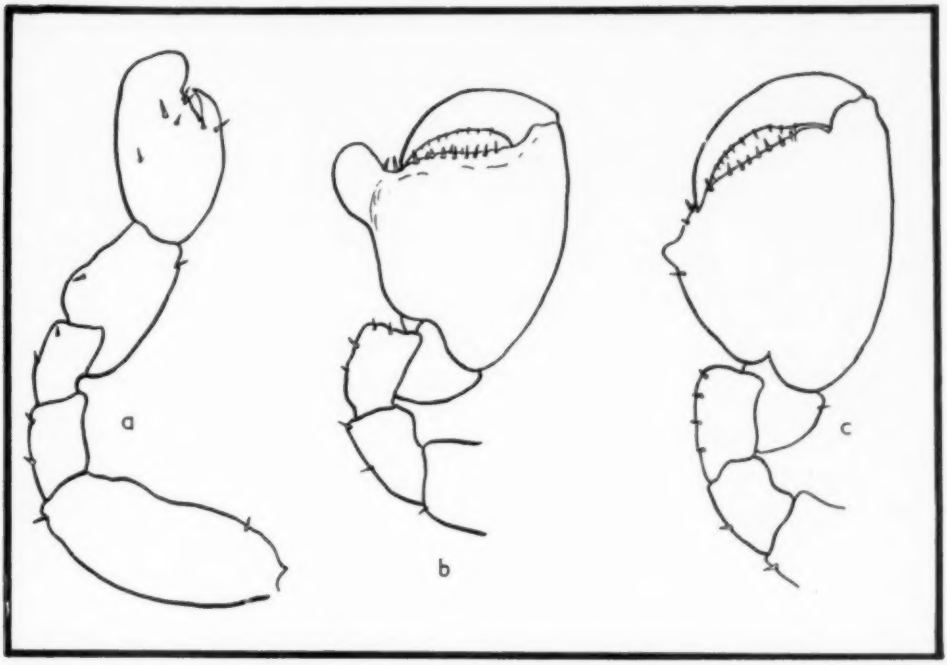

FIG. 2. *Talorchestia bottae*. Three successive stages in development of second gnathopod of male. (After Chilton, 1921.)

diet to that of the supralittoral species, this is not unexpected.

The gnathopod structure, however, does show certain modifications. Chilton, in an unpublished journal, writes of the "peculiar transparent portions of the merus, carpus, and propod" of the gnathopods of *Orchestia sylvicola* and asks, "What can be the function of these strange looking structures? In them, the integument appears semitransparent and usually more or less striated, and the joint bulges out at these places, but no muscles are to be seen in the enlargements."

Since these processes are absent from the male gnathopods in some species, it is unlikely that they are primarily connected with food or feeding habits; rather, reduction in size of the large second gnathopods from the condition found in marine and supralittoral species, and simultaneous development of processes in terrestrial species indicate changes in sexual habits as a primary cause. The most prominent features of the "pellucid lobes" are their lack of musculature, their transparency (partly due to the absence of muscle tissue), and their scabrous surface. They are situated on the lower margin of the limb which would scrape along the ground and be most exposed to external stimuli. These features all suggest to me a tactile sensory function. McIntyre, in an unpublished work, has described the value of the peculiarly twisted female second gnathopod, which is well supplied with these pellucid processes, in combing the broodplates.

In fact, it does seem likely that there has been a change in sexual habits. Williamson (1951) studied the mating and breeding of

some supralittoral or "semiterrestrial" amphipods, and found that in *Talitrus saltator* the female is held by the male with the aid of the stout antennae and the peraeopods, whereas "holding" in marine and supralittoral species is normally done with the aid of a greatly developed second gnathopod. *Talitrus saltator* is, however, the only species of *Talitrus* which shows this marked development of strong antennae. The other, more truly terrestrial, species of *Orchestia* and *Talitrus* have slender antennae. Since most of them also lack the large male "grasping hand" of the supralittoral species, it is likely that some further change in sexual habits has taken place. (A few terrestrial species retain the large "grasping hand.")

In the Gammaridae, the eggs are laid almost immediately after copulation, the time of laying in some species being determined by the time of copulation, in others by the time of moulting. In *T. saltator*, and probably in other talitrids, the time of laying is determined by the time of moulting. Laying takes place 4 days after moulting, but copulation may take place any time from 1 to 4 days before laying.

Williamson suggests that the eggs of the supralittoral Talitridae are fertilised in the brood pouch, and rules out both internal insemination and internal fertilisation. The spermatozoa, which are already present when laying takes place, are then most probably activated either by a secretion of the unfertilised egg or by a secretion which the female releases during laying. Spermatozoa of *T. saltator* can live at least 4 days in the brood pouch of the female, probably because of their inactivity and perhaps also because of their relatively large size (about 400 microns in length).

More tangible developments correlated with the terrestrial environment are evident. In aquatic species of Talitridae, the male normally carries the female around for some days before moulting, and copulation occurs immediately after moulting. "The carrying position adopted by . . . *Gammarus* . . . is obviously not suited to terrestrial conditions, . . . but it is probable that the aquatic ancestors of the Talitridae employed this form of carrying, and it is still found in the more aquatic members of the family (*Hyale* spp.)" (Williamson, 1951).

In the supralittoral species, there is no carrying before moulting. "Associated with the terrestrial habitat, therefore, we see not only modifications in the method of carrying, but also a great reduction in its duration" (Williamson, 1951).

From these facts, Williamson concludes that the delayed egg laying, associated with the longevity of the sperm, has an adaptive significance. Where the moult governs the time of laying, the delay increases the chances of mating by increasing the time, between moulting and laying, in which mating can take place; furthermore, the male does not have to carry the female. On the other hand, mating in aquatic forms "can take place over a period of several days before the moult, and the probability of mating would be very little increased if egg laying were delayed for a few hours, or even days, after the moult" (Williamson, 1951).

Correlated with the terrestrial environment, there is also a reduction in the number of eggs produced. In most species of terrestrial amphipods, I have found the number of eggs in the brood pouch ranges from 1 to 10, e.g., in *Talitrus sylvaticus* the average is between 3 and 4. Yet in marine genera of the same family, the number carried by an ovigerous female of similar size may be many times this. An *Allorchestes novizealandiae* female taken at random carried 161 eggs, the greater carrying capacity of the animal being in part due to the much smaller size of the eggs.

Sexton (1924) has shown a decrease in number of eggs produced by species of *Gammarus* from marine to pelagic species. *Gammarus locusta*, a marine species, has as many as 143 eggs in a brood. The brackish-water *G. chevreuxi* has 30–40 per brood; the fresh-

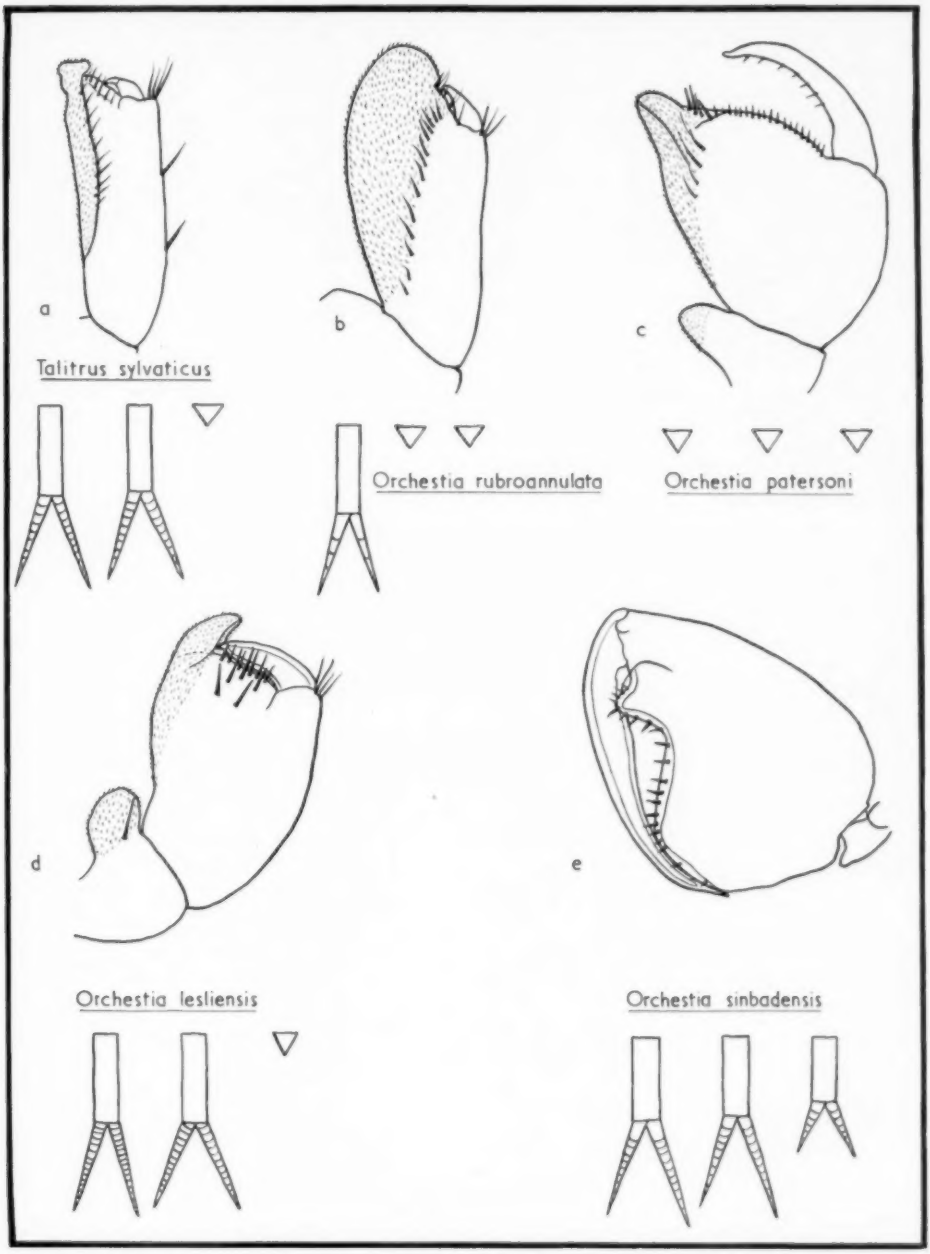

FIG. 3. Adult male second gnathopods of five species of terrestrial amphipods showing similarities to developmental stages of other species (cf. Fig. 2). Diagrammatic representations of the pleopods are given for each species. (The number of segments per ramus indicated corresponds to the number suggested by setation; in some species, actual segmentation appears superficial or incomplete.)

water *G. pulex*, 12–18; and a littoral species of *Gammarus*, 8–12. Lawrence (1953) gives a figure of 6–14 eggs for the terrestrial *Talitrus* (*Talitroides*) *eastwoodae*, "the average thus being almost identical with that of the littoral species quoted by Sexton." Lawrence further states that, as far as is known, there is only one annual brood in *T. eastwoodae*, whereas *G. chevreuxi* breeds all the year round. Sexton (1928) writes of one female *G. chevreuxi* which was known to have 29 broods in a lifetime—12 to 18 months is noted as the average breeding lifetime of a female *G. chevreuxi*—and Hynes (1955) says that *G. pulex* will breed five times in a year.

So, as in other groups of invertebrates which have adapted themselves to terrestrial or fresh-water life, the eggs tend to be larger and fewer, an example of the general tendency for the more advanced species of a group to be more sparing in the production of the young. It is reasonable to expect that, as in other advanced groups, the eggs and young will have a longer developmental period, but when launched from the protection of the parental brood pouch the young will be more mature than those of the marine species. It is significant that *Talitrus saltator* takes considerably longer to mature than the 2 to 2½ months required by the somewhat more hydrophilous *Orchestia gammarella* (Verwey, 1929, quoted by Williamson, 1951).

Thus, changes in sexual habits and breeding of the supralittoral species are directly advantageous in entering the terrestrial environment. The suggested trend in delaying of egg laying until after moulting is most significant, and one would expect the truly terrestrial species of *Talitrus* to have developed this trend even further, being limited ultimately only by the viability of the sperm.

MOISTURE REQUIREMENTS

Moisture requirements appear to have been met by the relatively stable nature of the environment. The nature of the leafmould zone itself does away with much of the necessity for special adaptations. I have found that terrestrial amphipods in cultures uncontrolled for humidity vary specifically in resistance to changes of moisture, as would be expected from similar work on isopods (Edney, 1951) but that all species are extremely susceptible to dessication. Apart from these variations in resistance, no specific adaptations to moisture requirements have been observed. Edney's work on isopods (1951, 1954) suggests that adaptations to this environmental factor are to be found in behavioural and physiological rather than morphological factors. He believes that terrestrial isopods have not developed the waxes characteristic of insect cuticles "which have contributed largely to their success as terrestrial animals."

However, there is evidence that such water-conserving adaptations as impermeable cuticles are not the only way of meeting the hazards of at least a limited degree of terrestrial life. "The ability to evaporate water rapidly, and thus to cool the body, may be of survival value when woodlice are exposed to high temperatures for short periods, particularly in littoral forms which may well have been intermediate in the evolution of terricolous from maricolous isopods" (Edney, 1951*a*). This is supported by various measurements of transpiration rates in cryptozoic invertebrates quoted in Edney (1954), suggesting that "high transpiration rates are generally associated with cryptozoic arthropods."

Casual observations support the likelihood that the permeability of the exoskeleton of terrestrial amphipods is much greater even than that in isopods, and by inference, that transpiration rates may also be higher. Terrestrial amphipods, when placed in 70–95 per cent alcohol, immediately react vigorously, but in little more than 10 seconds show no further signs of life. Isopods, under the same conditions, have been observed to react for as long as 10 minutes before final quiescence. I have also noted a similar differential rate in susceptibility to dessication. Lawrence (1953) likewise notes that *Talitrus eastwoodae*

may survive as long as 9 days in fresh tapwater, but "on the other hand it is much more susceptible to dry air in which it succumbs very quickly," a statement which incidentally raises questions regarding control of osmotic pressure within the body.

These points further emphasise a very important aspect of the ecology of the cryptozoic fauna, that "the forest community, by its very nature, solves the problem of water conservation for a host of plants and animals, making unnecessary for them the specific adaptations to economy of water that may be essential in other terrestrial environments" (Allee, Emerson, *et al.*, 1949).

EXCRETION

The excretory problems facing animals of marine origin which colonise the land are well known. Foremost amongst these is the retention of water, which requires the development of mechanisms for the resorption of water from excreta, and adaptation of the excretory end product. In most groups, this is expressed by a change in the major nitrogenous end product from the ammonia of marine groups to the urea or uric acid of terrestrial groups, with accompanying complexity of excretory organs.

Dresel and Moyle (1950) describe studies on nitrogenous excretion in amphipods and isopods, including a supralittoral species of *Orchestia*. They conclude that more than 50 per cent of the total soluble nonprotein nitrogen of the excreta is in the form of ammonia. "The level of nitrogen excretion is appreciably lower in the terrestrial species than in any of the others, indicating that, in this group, adaptation to terrestrial conditions has been attended by a general suppression of nitrogen metabolism rather than a transformation to other, less toxic products." Some excretion of uric acid, 5–10 per cent of the total soluble nonprotein nitrogen, took place in the terrestrial isopods. Associated with this excretion, "some retention of this insoluble compound usually occurs, and it was found that among the terrestrial species the amount so stored parallels the degree of morphological and physiological adaptation to terrestrial conditions. . . . It seems more plausible, however, to attribute this increased uric acid retention in the more xerophilous species to a reduced rate of excretion rather than to a fundamental difference in metabolism."

Thus, they conclude that "adaptation to terrestrial conditions [in the Isopoda and Amphipoda] has been attended by a general suppression of nitrogen metabolism rather than by a transformation of ammonia to other, less toxic products."

Apart from this work of Dresel and Moyle, nothing is known of excretory processes or mechanisms in the terrestrial amphipods.

OXYGEN CONSUMPTION

The rate of oxygen consumption in *Talitrus sylvaticus* has been investigated by Clark (1955). Apart from a decrease in rate of respiration relative to increase of body weight, which is normal for Crustacea, he found that oxygen consumption was relatively higher in winter than in summer, the winter consumption corresponding to that at a temperature 2.5°C. higher in summer. "Of the factors influencing the rate of oxygen consumption . . . first order interactions occurred between temperature and body weight, temperature and season, and season and body weight. There was also a significant second order interaction between temperature, body weight and season. . . . Adaptation . . . to oxygen uptake by *Talitrus sylvaticus* to seasonal differences in temperature was not sufficient to enable it to maintain the same rate of output of energy in winter as in summer" (Clark, 1955).

The occurrence of a seasonal adaptation of rate of oxygen uptake has been found only infrequently in invertebrates, and the necessary physiological mechanism is unknown.

RESPIRATION AND PLEOPOD STRUCTURE

It is interesting to compare the relationship

of the pleopods to respiration in the Isopoda and the terrestrial Amphipoda.

In the Isopoda, the pleopods show a series of modifications for respiratory purposes. In marine species, the pleopods are used both in swimming and for respiration. In the terrestrial species, as in the amphipods, they are no longer of use in locomotion. In the primitive state, both exopodite and endopodite in all pleopods are respiratory. In the Ligiidae, the exopodite is the primary respiratory organ and the endopodite is a secondary one. In the more primitive terrestrial species, such as in the Oniscidae, the endopodites are transformed into branchial lamellae and take over most of the respiratory function. In *Porcellio* and other genera, the exopodites have completely lost their respiratory function and act as lamellae protecting the endopodites from dessication. However, in the most advanced terrestrial species, the endopodites again regress and are replaced by pseudotracheae ("white bodies" or "tracheal glands") on the inner side of the exopodites. It is these pseudotracheae which enable the desert-dwelling species to survive. The pseudotracheae have evolved in three independent lines comparable to and surpassing the development of a terrestrial mode of life in the amphipod genera, *Orchestia*, *Talorchestia*, and *Talitrus*.

In marine species of amphipods, the pleopods have three functions (Watkins, 1930, 1940). They are used for *swimming*, they draw a constant current of water over the gills, and the same current, filtered by the gnathopods, serves as a food vehicle.

With the development of extensive pleon muscles and the change to a supralittoral jumping habit, pleopods are no longer used in feeding. Food is obtained actively and the gnathopods are used to grasp and convey it to the mouth. However, all supralittoral species possess fully developed pleopods, suggesting that they are still used in respiration. Since supralittoral species have not lost the power to swim and occasionally need to swim if they are to survive, their pleopods may fulfil two of these functions.

Among terrestrial species there is a trend towards reduction or complete loss of pleopods except for vestigial triangular stumps, but there are exceptions to this. New Zealand species from leafmould collected 2,000 to 3,000 feet above sea level have fully developed pleopods, e.g., *Orchestia sinbadensis* Hurley (1957).

A completely terrestrial habitat removes any need of pleopods for swimming. According to Lawrence (1953), *Talitrus eastwoodae* "never swims when placed in water and is evidently unable to raise itself above the bottom of a glass jar, moving round in it precisely the same way as if walking on dry land." The absence of pleopods in *O. patersoni* (Stephensen, 1938) implies that sufficient oxygen is available to the respiratory surfaces without need for a constant current of air created by the pleopods. As might be expected, there is in most species a considerable development of respiratory surfaces correlated with this loss. "The gills of the anterior pair of pereiopods are rather large, in the female especially so in pereiopod 2" (Stephensen, 1935). *Talitrus pilratus* is a good example of this marked development; it has the gills of the fourth pereiopod, as well as those of the second, much enlarged and elongated (Hurley, 1955). Possibly, the retention of pleopods in some terrestrial species depends on a burrowing habit, in which case the available air in the burrow might stagnate more rapidly were not the pleopods used to increase the circulation. A correlation has also been suggested between burrowing and reduction of eyes, or even loss of pigment, as in *Orchestia marincana* (Stephensen, 1935), but evidence of this is very limited.

OTHER MODIFICATIONS

In the Isopoda, at the same time as the developments in the pleopods described above, other tendencies have appeared. The antennae have become reduced, probably with an as-

sociated loss of sensory perception; the body in many species has become capable of rolling into a ball, or "conglobating," thus giving the animal greater protection from desiccation and, presumably, from its natural enemies; and locomotory powers have been reduced by weakening of the peraeopods (Van Name, 1936:282,328). In the terrestrial Amphipoda, the antennae are much simpler than in most marine and littoral species; they are more slender; they lack calceoli and other similar sensory structures; but there does seem to be a development of fine setae of a tactile nature. Terrestrial species are extremely mobile. There is no morphological adaptation to protect the gills—if anything they are more exposed by reason of their greater length; nor is there any sign of structural adaptation like the "conglobating" power of isopods. However, with increase in gill size, as in *Talitrus sylvaticus*, it would not have been unreasonable to have expected some physiological or morphological modification analogous to the development of pseudotracheae in the terrestrial isopods. It is probably because of the lack of just such modifications that the terrestrial amphipods, seemingly well suited for the leafmould environment, have not occupied other, more stringent niches.

What has been said of the terrestrial isopods, also may be said of the amphipods: "Any success which the group enjoys on land is due, not so much to the development of characters conferring independence of the environment, but to behavioural mechanisms which keep them for the most part in moist, cool places. . . . The general picture which emerges is of a group of animals comparatively ill equipped for life on land. All the devices which permit such existence are in some degree makeshift. . . . And yet, despite these disadvantages, the animals are by no means uncommon, and there is little doubt that the success which they do enjoy is the result not so much of morphological or physiological adaptations as of behavioural mechanisms which restrict them to the cryptozoic niche where the rigours of true terrestrial existence, as well as its opportunities, are avoided" (Edney, 1954).

SUMMARY

The term "supralittoral" is applied to Amphipoda of the seashore zone; "terrestrial" is restricted to those species which are entirely independent of sea water. Almost all of these are leafmould species which are characteristic of, and restricted to, the Indo-Pacific islands and land masses. The terrestrial amphipods have colonised the land directly from the littoral zone. The forest floor provides the relatively stable conditions which assist colonisation and provide considerable protection in unfavourable times. Drastic changes in feeding habits have not been necessary.

Adaptations which have taken place or seem most likely to have occurred are these:

1. Feebly chelate gnathopods in *Talitrus* and reduced male second gnathopods in *Orchestia* species are correlated with changes in sexual habits, the development of large second gnathopods in the male to hold the female during copulation having been lost. In *Talitrus saltator* stout antennae are used for this purpose, but in most terrestrial amphipods the antennae are long and slender, and there must have been a further, as yet undescribed, change in sexual habits. Scabrous pellucid areas on the male gnathopods, characteristic of terrestrial amphipods, are probably of tactile sensory nature and possibly correlated with feeding habits.

2. There is a tendency for the male second gnathopod in mature animals of some species to resemble the immature males in other, less terrestrial, species. It is suggested that species formation in terrestrial amphipods is correlated with neotony.

3. There is evidence that males are comparatively few in some terrestrial populations, although this may be true only of certain species and times of the year.

4. Fewer but larger eggs are produced by

of the pleopods to respiration in the Isopoda and the terrestrial Amphipoda.

In the Isopoda, the pleopods show a series of modifications for respiratory purposes. In marine species, the pleopods are used both in swimming and for respiration. In the terrestrial species, as in the amphipods, they are no longer of use in locomotion. In the primitive state, both exopodite and endopodite in all pleopods are respiratory. In the Ligiidae, the exopodite is the primary respiratory organ and the endopodite is a secondary one. In the more primitive terrestrial species, such as in the Oniscidae, the endopodites are transformed into branchial lamellae and take over most of the respiratory function. In *Porcellio* and other genera, the exopodites have completely lost their respiratory function and act as lamellae protecting the endopodites from dessication. However, in the most advanced terrestrial species, the endopodites again regress and are replaced by pseudotracheae ("white bodies" or "tracheal glands") on the inner side of the exopodites. It is these pseudotracheae which enable the desert-dwelling species to survive. The pseudotracheae have evolved in three independent lines comparable to and surpassing the development of a terrestrial mode of life in the amphipod genera, *Orchestia*, *Talorchestia*, and *Talitrus*.

In marine species of amphipods, the pleopods have three functions (Watkins, 1939, 1940). They are used for swimming, they draw a constant current of water over the gills, and the same current, filtered by the gnathopods, serves as a food vehicle.

With the development of extensive pleon muscles and the change to a supralittoral jumping habit, pleopods are no longer used in feeding. Food is obtained actively and the gnathopods are used to grasp and convey it to the mouth. However, all supralittoral species possess fully developed pleopods, suggesting that they are still used in respiration. Since supralittoral species have not lost the power to swim and occasionally need to swim if they are to survive, their pleopods may fulfil two of these functions.

Among terrestrial species there is a trend towards reduction or complete loss of pleopods except for vestigial triangular stumps, but there are exceptions to this. New Zealand species from leafmould collected 2,000 to 3,000 feet above sea level have fully developed pleopods, e.g., *Orchestia sinbadensis* Hurley (1957).

A completely terrestrial habitat removes any need of pleopods for swimming. According to Lawrence (1953), *Talitrus eastwoodae* "never swims when placed in water and is evidently unable to raise itself above the bottom of a glass jar, moving round in it precisely the same way as if walking on dry land." The absence of pleopods in *O. patersoni* (Stephensen, 1938) implies that sufficient oxygen is available to the respiratory surfaces without need for a constant current of air created by the pleopods. As might be expected, there is in most species a considerable development of respiratory surfaces correlated with this loss. "The gills of the anterior pair of pereiopods are rather large, in the female especially so in pereiopod 2" (Stephensen, 1935). *Talitrus sylvaticus* is a good example of this marked development; it has the gills of the fourth peraeopod, as well as those of the second, much enlarged and elongated (Hurley, 1955). Possibly, the retention of pleopods in some terrestrial species depends on a burrowing habit, in which case the available air in the burrow might stagnate more rapidly were not the pleopods used to increase the circulation. A correlation has also been suggested between burrowing and reduction of eyes, or even loss of pigment, as in *Orchestia marquesana* (Stephensen, 1935), but evidence of this is very limited.

OTHER MODIFICATIONS

In the Isopoda, at the same time as the developments in the pleopods described above, other tendencies have appeared. The antennae have become reduced, probably with an as-

sociated loss of sensory perception; the body in many species has become capable of rolling into a ball, or "conglobating," thus giving the animal greater protection from desiccation and, presumably, from its natural enemies; and locomotory powers have been reduced by weakening of the peraeopods (Van Name, 1936:282,328). In the terrestrial Amphipoda, the antennae are much simpler than in most marine and littoral species; they are more slender; they lack calceoli and other similar sensory structures; but there does seem to be a development of fine setae of a tactile nature. Terrestrial species are extremely mobile. There is no morphological adaptation to protect the gills—if anything they are more exposed by reason of their greater length; nor is there any sign of structural adaptation like the "conglobating" power of isopods. However, with increase in gill size, as in *Talitrus sylvaticus*, it would not have been unreasonable to have expected some physiological or morphological modification analogous to the development of pseudotracheae in the terrestrial isopods. It is probably because of the lack of just such modifications that the terrestrial amphipods, seemingly well suited for the leafmould environment, have not occupied other, more stringent niches.

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2. There is a tendency for the male second gnathopod in mature animals of some species to resemble the immature males in other, less terrestrial, species. It is suggested that species formation in terrestrial amphipods is correlated with neotony.

3. There is evidence that males are comparatively few in some terrestrial populations, although this may be true only of certain species and times of the year.

4. Fewer but larger eggs are produced by

terrestrial than by aquatic species of the same family, and there is a longer growth and breeding period. Carrying of the female by the male for long periods is obviated and may be entirely lacking, and the time after egg laying during which fertilisation is possible has been lengthened, thereby increasing the chances of mating. This would greatly facilitate entry into the terrestrial environment, especially since it appears first in supralittoral species.

5. There is a tendency for pleopods to be reduced to vestigial stumps, although species found high above sea level may have fully developed pleopods. Their absence in some species suggests that sufficient air is available to the respiratory surfaces without need of a pleopod-created current of air over the gills. In some species there is a marked development in size of gills.

6. The terrestrial species show strong evidence of endemism. This is probably due partly to the nature of their environment and partly to lack of available transport as compared with marine and littoral species, although the advent of man has complicated distribution patterns to some degree. In at least two genera, *Talitrus* and *Orchestia*, terrestrial species have arisen independently from littoral species.

7. Moisture requirements are met by the leafmould environment and behavioural patterns of the animals.

8. There is some evidence that excretory problems have been solved, not by a change in end products of excretion, but by a general slowing down and suppression of nitrogen metabolism.

9. The leafmould environment provides conditions most favourable to colonisation by a marine or littoral group of animals and requires a minimum of physiological or morphological adaptations.

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean
Part IV. Various Small Collections from the Central Pacific Area, including Supplementary Notes on Alpheids from Hawaii[1]

ALBERT H. BANNER[2]

IN THE COLLECTIONS made available to me are a number of small collections, in some cases only single specimens, made from various islands ranging from the Tuamotus to the Carolines, none being extensive enough to warrant separate papers. Some of these have been loaned by the United States National Museum, some by the Bernice P. Bishop Museum, and some by the individual collectors, e. g., the collection by R. W. Hiatt from the islands of Yap. Also, in the continuing collections made in Hawaii since the completion of my 1953 paper, three additional species have been found and two notable variations in the usual form or color of known species have been observed. Finally, a new name has been applied to a species previously described from Hawaii.

Because the specimens came from such widely separated localities and because so few species came from each collection, the collection data are listed under each species rather than in a preliminary comprehensive collection list, as has been done in previous articles.

As in previous papers in this series, instead of repeating the full synonymy for species which have been discussed in previous papers, I have made reference to the earlier papers in the series which have presented the synonymy.

The collections were made for numerous sponsors, some of whom have been forgotten in the many years since the collections were made. This study has been done largely under a grant to the author from the National Science Foundation (NSF G-1754).

Type specimens of the new species described in this paper will be deposited in the institution from which they were borrowed; those types in my personal collection will be deposited either in the Bernice P. Bishop Museum or in the U. S. National Museum (USNM).

ARETE Stimpson

Arete dorsalis Stimpson

Arete dorsalis Stimpson, Acad. Nat. Sci. Phila., Proc. 12: 32, 1860.

LOCALITIES: 1 specimen, Station 1847, Raroia Atoll, Tuamotu Archipelago, "from green-black sea urchin from middle zone of outer reef flats Ngarumaoa Island. . . "; collected by J. E. P. Morrison, July 5, 1952. Four specimens from Station 1857, collection data as above.

DISCUSSION: These specimens will be discussed in a future paper dealing with this genus and the genus *Athanas* Leach.

Arete indicus Coutière

Arete dorsalis var. *indicus* Coutière, Soc. Philomath. Paris, Bul. IX, 5(2): 85, figs. 25–30, 1903.

Arete indicus Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2: 863, figs. 134–135, 1905.

[1] Contribution No. 111, Hawaii Marine Laboratory.

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TABLE 1
COLLECTION DATA FOR SPECIMENS STUDIED

LOCATION AND COLLECTOR'S NUMBER	ISLAND	ARCHIPELAGO	COLLECTOR	LOANING AGENCY
Tomil Harbor, Nos. Y-111, 122, 214, 215, 252	Yap	Caroline	R. W. Hiatt	R. W. Hiatt
No. 2063	Oneroa	Caroline	Morrison, Doty, Herre	USNM
Kwajalein Atoll	Kwadak	Marshall	P. E. Cloud, Jr.	USNM
Likiep Atoll, No. 827	Nado	Marshall	S. V. MacNeil	USNM
No. 1742	Canton	Phoenix	E. H. Bryan	Bishop Museum
	Jarvis	Line Islands	Toomey, Ahia, Graf	Bishop Museum
	Washington	Line Islands	C. H. Edmondson	Bishop Museum
	Palmyra	Line Islands	C. H. Edmondson	Bishop Museum
No. 3707	Midway	Hawaiian	C. H. Edmondson	Bishop Museum
Nos. 1497, 1498	Wake		C. H. Edmondson	Bishop Museum
	Wake		C. H. Edmondson	Bishop Museum
Pearl and Hermes Reef		Hawaiian	U. S. Navy Ship "Dranga"	Bishop Museum
	Midway	Hawaiian	Y. D. P. Speicer	Bishop Museum
Kaneohe Bay	Oahu	Hawaiian	A. H. Banner	
Ahoolaka, Kaneohe Bay	Oahu	Hawaiian	A. H. Banner	
Wailupe pond	Oahu	Hawaiian	Donald C. G. McKay	Donald C. G. McKay
Raroia Atoll, No. 1847	Ngarumaoa	Tuomotu	J. P. E. Morrison	USNM
Raroia Atoll, No. 2015	Otikaheru	Tuomotu	J. P. E. Morrison	USNM
Raroia Atoll, No. 2187	Kakipuku	Tuomotu	J. P. E. Morrison	USNM
Raroia Atoll, No. 2252	Ngarumaoa	Tuomotu	Maxwell Doty	USNM
Raroia Atoll, No. 1963	Hamahomo	Tuomotu	J. P. E. Morrison	USNM

LOCALITY: 1 specimen, Station 2187, Kakipuku Island, Raroia Atoll, Tuamotu Archipelago, from boring sea urchin; collected by J. E. P. Morrison, August 26, 1952.

DISCUSSION: This specimen, although it lacks all of its appendages, has been put in this species because it compares so well with specimens plainly of this species from the same habitat (holes made by the sea urchin *Echinometra*) collected from Aitutake, Cook Islands. This species will be discussed in a later paper.

SALMONEUS Holthius

Salmoneus tricristata sp. nov.
Fig. 1*a–e*

LOCALITY: 1 specimen, Station Y-122, Tomil Harbor, Yap Island, Caroline Archipelago, an ovigerous female 12 mm. long lacking large chela, having one each of 2nd, 3rd, and 5th legs, and both 4th legs; collected by R. W. Hiatt, 1946.

DESCRIPTION: Rostrum with tip reaching to end of second antennular article, anteriorly narrow but broad at base. Orbital teeth about one-third length of rostrum, tips acute. Both orbital hoods and rostrum bearing dorsal keels, that of the rostrum extending posteriorly from tip to more than two-thirds the length of the carapace, those of the orbital hoods extending almost to the tip of the hood and somewhat shorter than rostral carina.

Antennular articles short and broad. Stylocerite reaching to end of second antennular article. Scaphocerite broad and rounded, lateral spine equal in length to rounded anterior portion.

Large chela lacking. Merus of small chela about 4.5 times as long as broad, broadest in middle; carpus equal in length and breadth to merus, but widest distally; palm a little less than half as long as carpus; fingers equal in length to palm.

First carpal article of second legs slightly longer than the sum of the four distal articles.

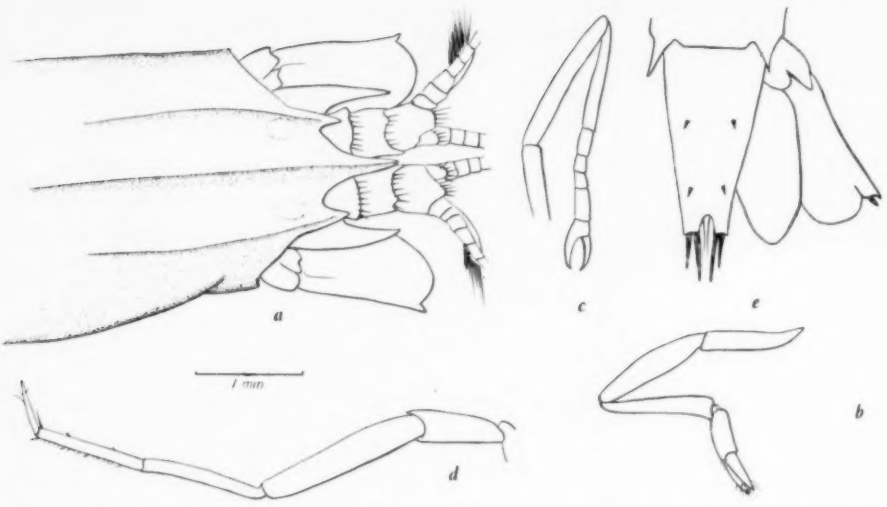


FIG. 1. *Salmoneus tricristata* sp. nov. *a*, Anterior region, dorsal aspect; *b*, small chela; *c*, second leg; *d*, third leg; *e*, telson and uropod. All drawn to same scale.

Third legs with ischium half as long as merus, a little more than twice as long as broad; merus 5 times as long as broad, unarmed; carpus about two-thirds as long and less than half as broad as merus; propodus slightly shorter and thinner than carpus, armed with 4 feeble spines on superior margin and two similar spines on inferior, armed on distal inferior margin with a longer and heavier movable spine; dactylus half as long as propodus, slender, tapering and with a slight curve.

Telson with anterior margin 2.5 breadth of posterior margin and length 4.5 times the posterior breadth; sides with uniform taper; terminal cleft one-ninth length of telson. Tip of telson armed with two pairs of spines, the inner as long as the tip is broad and the outer two-thirds the length of the inner. Cleft bearing two setae. Spines of dorsal surface of telson rather weak.

DISCUSSION: The original name of this genus, *Jousseaumea*, has been changed by Holthius (1955:88) to *Salmoneus*, as the original name was preoccupied.

With Coutière's entirely inadequate description of his three species it is difficult, if not impossible, to be certain of any species. His original description of *Jousseaumea latirostris* (1896:382) was:

"Les épines supra-oculaires sont très peu marquées et le rostre très large. L'une des pattes antérieures manque." In 1897 (p. 234) he added that the large chela was like that of *J. serratidigitus* Coutière, and in 1899 (p. 71, fig. 21) he supplied a dorsal view of the anterior carapace.

As a consequence, until the three species described by Coutière are redescribed adequately, every new species must be regarded as tentative. This species appears to be unique in the possession of the three crests on the anterior half of the carapace. *S. cristata* (Coutière) may have a somewhat similar medial crest, but the two lateral crests represent the continuation of the lateral margins of the rostrum and do not arise from the corneal teeth as do the ones on this species. Other species have the rostral crest, like *S. hilarula* (de Man), but in them it does not extend as

far posteriorly as it does on this species; *S. brevirostris* (Edmondson) has also the crests from the corneal teeth, but again, these do not extend far posteriorly and are not parallel.

If the development of the crests is consistent within a species, and if the interpretation of Coutière's sketches and brief descriptions are correct, this can be regarded as a separate species.

SYNALPHEUS Bate

Synalpheus coutierei Banner

Synalpheus biunguiculatus Coutière (*nec* Stimpson), Soc. Ent. de France, Bul. (11): 232, figs. 1–4, 1898.

Synalpheus coutierei Banner, Pacific Sci. 7(1): 36, 1953.

LOCALITY: 1 specimen, Bernice P. Bishop Museum No. 1742, Canton Island, Phoenix Archipelago; collected by E. H. Bryan, 1924.

DISCUSSION: While this specimen is definitely *S. coutierei*, it differs slightly in the rostrum and antennular peduncle from the illustration of Coutière. In his figures the orbital hoods are thinner than those in this specimen (which even exceeds the breadth as shown for *S. pachymeris*, *loc. cit.*, fig. 9) and the rostrum is definitely shorter than the orbital teeth and relatively thinner. In the antennular peduncle the articles are thinner and longer, but not markedly so, while the relative proportions of the parts of the antennular peduncle remain about the same. Considering the variation in the genus and the variation already reported for *S. coutierei*, this is probably not important.

Synalpheus carinatus (de Man)

Alpheus carinatus de Man, Arch. f. Naturgesch., 53: 508, pl. 22, fig. 2, 1887.

LOCALITY: 4 specimens, Kwadak, Kwajalein Atoll, Marshall Islands, from specimens of *Comanthus bennetti* (Müller) as determined by A. H. Clark, U. S. National Museum; collected by P. E. Cloud, Jr.

Synalpheus charon obscurus Banner

For synonymy, see Banner, Pacific Sci. 10(3): 329, 1956.

LOCALITIES: 1 specimen, Bishop Museum No. 3707, from Midway Island, Hawaiian Archipelago; 1 specimen, Bishop Museum No. 1497, from Wake Island (19°18′ N., 166° 35′E.), in coral; both collected by C. H. Edmondson, Tanager Expedition, 1923.

DISCUSSION: These specimens plainly belong to the new subspecies; the specimen from Midway, an ovigerous female, is 20 mm. long, the largest specimen yet seen.

Synalpheus paraneomeris Coutière

For synonymy, see Banner, Pacific Sci. 10(3): 331, 1956.

LOCALITIES: 2 specimens at Station 287, USNM 194726, from Likiep Atoll, Nado Island, Marshall Islands; collected by S. V. MacNeil. Two specimens from Jarvis Island, Line Islands; collected by Toomey, Ahia, and Graf, Itaska Expedition, 1935. One specimen from Wake Island; collected by C. H. Edmondson, Tanager Expedition, 1923.

DISCUSSION: The large chela of the male specimen from Wake Island has a ratio of the chela length to the finger length of 2.6, the longest finger yet encountered (see Banner, *loc. cit.*). The specimen otherwise agrees with the variable characteristics of this species.

Synalpheus tuthilli sp. nov.
Fig. 2*a–j*

TYPE SPECIMEN: An ovigerous female 12.6 mm. long, Station Y-215, Tomil Harbor, Yap Island, Caroline Archipelago; collected by R. W. Hiatt, 1946. An allotype, 10.5 mm. long, and 7 paratypes from same station.

DESCRIPTION: Rostrum short, reaching less than one-third the length of the visible portion of first antennular article; sides straight, with uniform taper, orbital teeth short, slightly shorter than rostrum, tips rounded, both medial and lateral margins slightly concave.

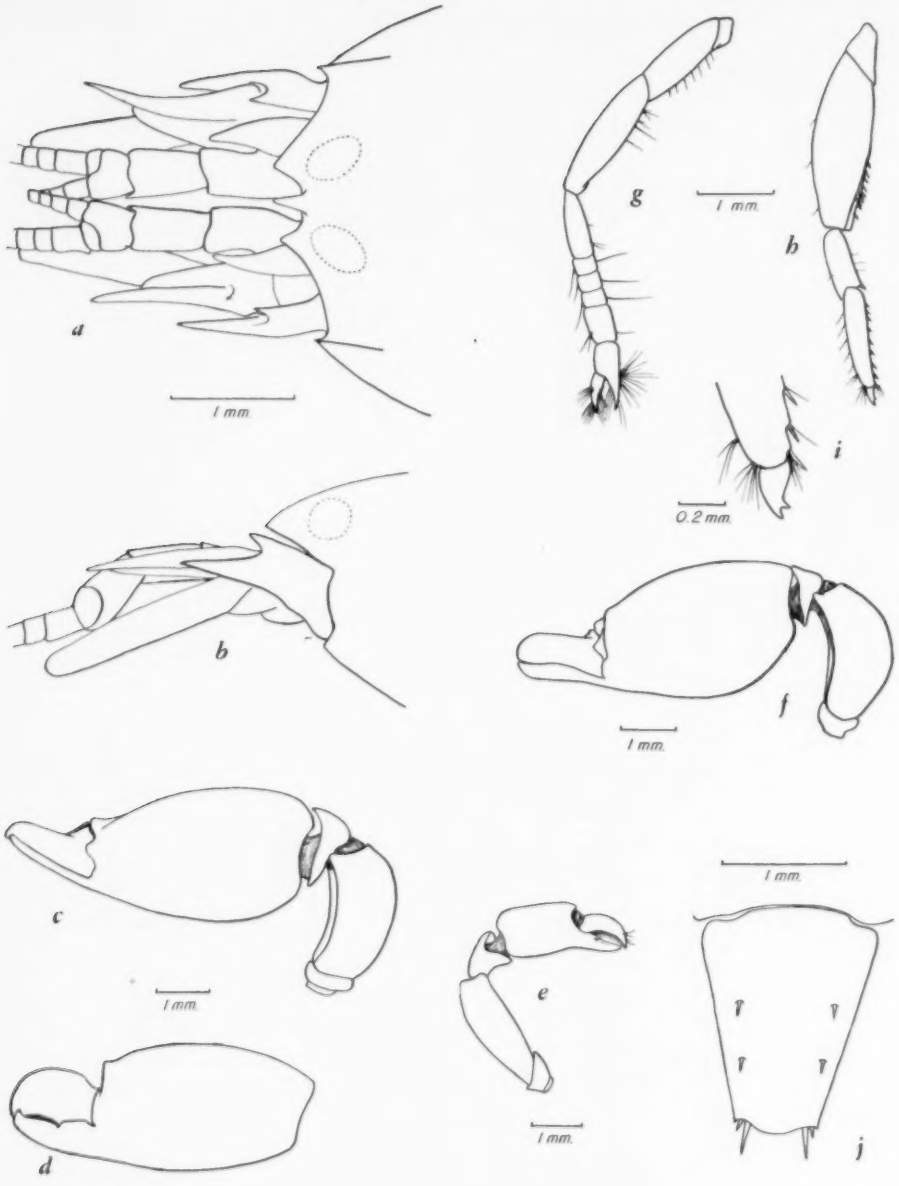


FIG. 2. *Synalpheus tuthilli* sp. nov. *a*, *b*, Anterior region, dorsal and lateral aspects (assymetry of scaphocerites are as found in specimen); *c*, large cheliped, female, lateral aspect; *d*, same, superior face; *e*, small cheliped, female; *f*, large cheliped, male; *g*, second leg; *h*, third leg; *i*, third leg, dactylus; *j*, telson.

Orbital hoods and rostrum depressed and rounded in lateral view.

Antennular peduncle with first article slightly longer than second; second article about twice length of third article. Stylocerites heavy, with slightly rounded tips not reaching to end of first antennular article. Lateral spine of basicerite reaching almost to middle of second antennular article. Stylocerite with lateral spine well developed (that of right side distorted on type specimen), reaching to end of antennular peduncle; blade reduced, narrow and reaching only to end of second antennular article. Carpocerite markedly longer than antennular peduncle.

Large chela inflated, subcylindrical in section, 2.4 times as long as broad, tapering strongly to fingers. End of palm above dactylar articulation unmarked by any prominences. Fingers occupying distal quarter of entire length of chela, twisted from axis of palm; dactylus high, narrow, with superior edge rounded. Merus short, less than half length of chela, heavy, twice as long as broad, and strongly curved, with superior margin more strongly curved than inferior; superior margin not terminated in angle, but curved towards dactylar articulation.

Small chela small but heavy, with palm 1.6 times as long as broad, and 1.7 times as long as fingers; fingers tapering, slightly broadened proximally. Merus about as long as that of large cheliped, almost as long as small chela proper; superior margin curved but not as strongly as that of large cheliped; inferior margin straight.

Carpal articles of second leg with ratio: 10:2.5:2.5:2.5:6.

Third legs with merus heavy, three times as long as broad, with inferior distal margin bearing numerous short spines which are usually concealed in normal side view by larger outer (or posterior) ridge. Carpus as long as merus is broad, superior margin ending in rounded tooth, inferior margin terminally armed with single weak spine. Propodus 0.56 as long as merus, 4.5 times as long as broad, armed with 9 weak spines. Dactylus less than 0.2 length of propodus, with strong taper and small ungui.

Telson 2.7 times as long as broad at posterior margin, with anterior margin twice as broad as posterior; lateral margins slightly convex in middle, terminated by slight subacute angles; posterior margin with low convexity.

DISCUSSION: In the nine specimens in the collection little variation is present except for the large chela and the armature of the merus of the third legs. In the larger specimens the length of the finger in respect to the chela is like that of the type, but in some of the smaller specimens the fingers occupy up to 0.32 the length of the chela; the fingers of the small specimens are also more slender, being as much as 2.6 times as long as broad. It should also be noted that the merus of the allotype is more strongly curved than that of the type. The merus of the third legs bears from 3 to 9 spinules, with the small number being on the smaller specimens.

It is also interesting that of this small collection, two males and one female (ovigerous) bear parasitic isopods on their abdomens.

This form is plainly related to *S. pachymeris* Coutière (1905*a*: 873) and *S. bituberculatus* de Man (1910: 294), and less closely to *S. coutierei* Banner (1953: 36) of the Coutierei group (see description under the name *S. biunguiculatus* (Stimpson) in Coutière, 1898: 230). The last species differs from the first two and from this form in that the merus of the third legs is unarmed. This form differs from the first two species in that the margin of the palm above the dactylar articulation is unarmed and the palm itself is inflated, while in both others the palm is more slender and bears one (*S. pachymeris*) or two (*S. bituberculatus*) rounded projections above the dactylus. There are also slight differences in the armature of the anterior carapace, but it is unlikely that these are of significance. In *S. pachymeris* and *S. bituberculatus* (but not in *S. pachymeris cargadosi* Coutière) the stylocerites are longer than the

first antennular article, but they are shorter in this form. Coutière regarded the number of spinules on the merus of the third legs as important in his description of his variety *S. p. cargadosi* (1921: 417), but neither in de Man's species, nor in Coutière's original description (where he described *pachymeris* as a variety of *S. biunguiculatus* = *S. coutierei*), any more than in these specimens, were the number of spinules constant between individuals.

Unfortunately the name *tuthilli* used in the genus *Alpheus* will have to be put in synonymy in a subsequent paper; this is another attempt to express thanks to Dr. Leonard D. Tuthill, friend and former editor of *Pacific Science*, for the help he has given me.

ALPHEUS Fabricius

Megacheles Group

Alpheus lanceostylus sp. nov.

Fig. 3*a–b*

Alpheus species 1, Banner, Pacific Sci., 10(3): 338, 1956.

TYPE: 28 mm. male collected at Pearl and Hermes Reef, Hawaiian Archipelago (27°N., 146°W.), by U. S. Navy Ship "Dranga" in 1927. Bernice P. Bishop Museum No. 2737.

PARATYPE: An ovigerous female 22 mm. long without chela collected from Saipan, Marianas (probably from the reef flat west of Cape Nafutan—exact data are lost), by A. H. Banner in 1945.

DESCRIPTION: Rostrum acute, reaching beyond end of first antennular article, broad at the base, dorsally only slightly rounded. Orbitorostral borders slightly concave. Orbital teeth strong, similar in shape to rostrum and about half as long.

Antennular peduncle with the second article 1.6 times the length of the visible portion of the first article, 1.2 times the length of the second article, and 1.3 times as long as broad. Stylocerite acute and reaching to middle of second antennular article. Scaphocerite broken on right side, left side with broad squamous portion reaching almost to tip, and tip slightly exceeding end of third antennular article. Carpocerite reaching slightly beyond end of scaphocerite. Lateral spine of basicerite not heavy, and reaching to level of tip of rostrum.

Merus of large cheliped with inner face 1.5 times as long as maximum breadth distally; superior margin terminating in subacute tooth; inferior external margin irregular but not bearing spines; inferior internal margin bearing 10 small movable spines and terminating distally in strong acute tooth. Ischium bearing 4 inferior spines and a strong superior tooth. Carpus bearing a rounded tooth on superior internal distal margin. Chela heavy, compressed, almost as broad distally through the fingers as proximally, 2.9 times as long as broad. Superior crest of palm terminating distally in strong acute tooth, interrupted by shallow and poorly defined transverse groove, and proximally merging with surface of chela. Superior groove shallow and flattened. Palmar crest broadly rounded and poorly defined proximal to transverse groove. Palmar groove broad and rounded. Inferior crest distinct only distally and ending in strong tooth. Inferior depression deep but rounded. Shoulder distinct but not abrupt. (For explanation of terms see Banner, 1953, fig. 17e). Fixed finger strongly curved. Dactylus closing across end of chela, thin with high sharp crest, and strongly curved; superior margin without marked lobes, inferior margin with what appears to be an extra rounded tooth. Cheliped bearing only scanty setae except near fingers where setae are somewhat heavier.

Small chela lacking in both type and paratype.

Carpal article of second legs with ratio 10:7:4:3:5.

Third legs with ischium bearing movable spine; merus 6.6 times as long as broad, unarmed; carpus unarmed and 0.5 length of merus; propodus bearing 7 weak spines, 0.7 as long as merus; dactylus slender, curved, with single superior serration.

Telson 1.4 times as broad proximally as distally, 2.5 times as long as tip is broad, with

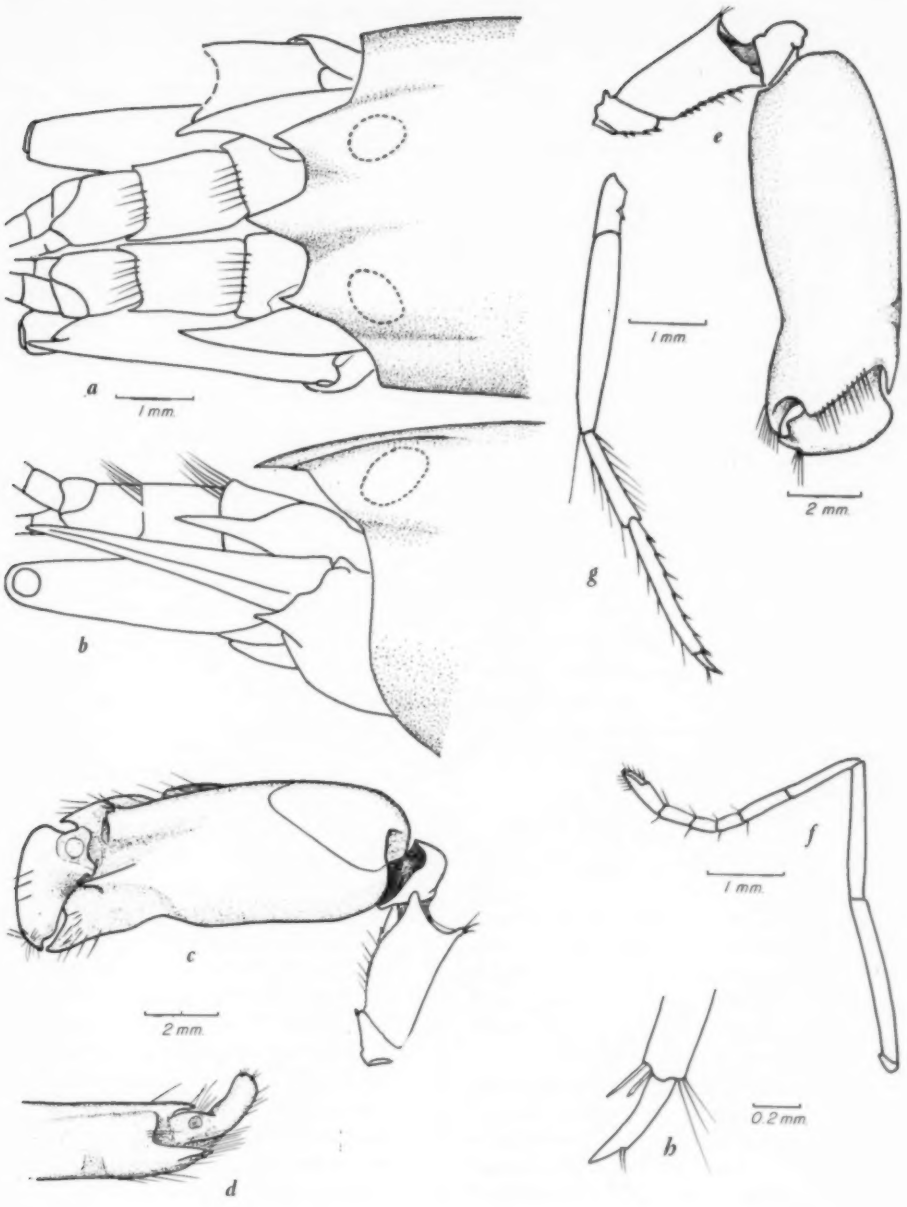


FIG. 3. *Alpheus lanceostylus* sp. nov. *a*, *b*, Anterior region, dorsal and lateral aspect; *c*, *d*, large cheliped, lateral and medial aspect; *e*, large chela, tip, superior aspect; *f*, second legs; *g*, third legs; *h*, third leg, dactylus.

lateral margins almost straight. Anterior dorsal spinules 0.3, posterior 0.6, of the length from articulation to tip.

DISCUSSION: The only difference noted between the incomplete specimen from Saipan and the type is that the propodus of the third legs carries 9 instead of 7 spines.

This species plainly belongs to the Megacheles group, and to the *A. hailstonei* Coutière complex (see Banner, 1953, p. 51 *et seq.*). However, it can be sharply separated from all others of that group (including *A. staphylinus* Coutière) by a series of characters, which include the broad second article of the antennular peduncle, the long stylocerite, and the nature of and direction of closure of the dactylus of the large cheliped. Other characteristics will separate it from one or more of the complex, as the presence of ischial spines will separate it from *A. hailstonei hailstonei* Coutière and *A. brachymerus* (Banner); the armature of the dactylus from several others, etc. (*op. cit.*, p. 55).

It is difficult to state which of the known species of the complex is most closely related to the new species. On the basis of the anterior carapace, large chela, and third leg it appears to be closest to *A. hailstonei paucispinata* (Banner).

Alpheus collumianus medius Banner

For synonymy, see Banner, Pacific Sci. 10(3): 340, 1956.

LOCALITIES: 2 specimens, Station Y-215, Tomil Harbor, Caroline Archipelago; collected by R. W. Hiatt. One specimen, Jarvis Island, Line Islands, Itaska Expedition; collected by Toomey, Ahia, and Graf, 1935. One specimen, Wake Island (19°18′N., 166° 35′E.), collected by C. H. Edmondsom, Tanager Expedition, 1923.

DISCUSSION: Of the two specimens from Tomil Harbor, Yap, one was similar to the type in all respects, but the other, also similar, showed assymetry in the basicerites, with one normal for the subspecies and the other like that of *A. c. inermis* Banner (1956:342).

The one specimen from Midway was also very similar to the type specimens except that its only remaining second leg had the carpus divided into six rather than five articles. The ratio of these articles was 10:2:9:4:4:7, showing that the extra article was the short one between the first and second articles.

Alpheus seurati Coutière
Fig. 4

Alpheus seurati Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 881, pl. 75, fig. 20, 1905.

LOCALITY: 1 specimen from Jarvis Island, Line Islands; collected by Toomey, Ahia, and Graf, Itasca Expedition, 1935.

DISCUSSION: This sole specimen of the species agrees almost perfectly with the description and figures of Coutière, although it lacks the small chela.

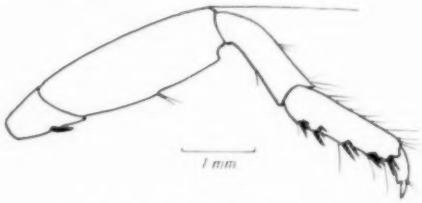


FIG. 4. *Alpheus seurati* Coutière. Third leg.

This species is plainly most closely related to *A. collumianus* Stimpson and within *A. collumianus* to the two subspecies, *A. c. medius* and *A. c. inermis* Banner (1956: 340). Coutière points out that the form of the anterior carapace, the large chela, the second legs, and the telson are like *A. collumianus* (actually, more like *A. c. medius*); the differences lie in the stylocerite—which is like that of *A. c. inermis*—and in the third legs, where the merus is broadened and lacking an acute distal tooth, but bears rather a rounded protuberance. He also points out several other characteristics that differ, but these, like the relative lengths of the second legs and the presence or absence of spines on the carpus of the third legs, are

variable characteristics, at least between the present subspecies.

I believe, therefore, that if the two subspecies are acceptable this species, too, should be made a subspecies of *A. collumianus;* however, I have deferred the action until more specimens can be examined.

Macrochirus Group

Alpheus huikau nom. nov.
Fig. 5*a–e*

Crangon nanus Banner, Pacific Sci. 7(1): 90, figs. 30, 31, 1953.

Alpheus nanus Banner, Pacific Sci. 10(3): 345, 1956.

nec Crangon nanus Krøyer, Naturhist. Tidsskr. 4(3): 231, 1842.

LOCALITIES: 13 specimens, Station 827, USNM 194726, Nado Island, Likiep Atoll, Marshall Islands; collected by S. V. MacNeil, 1952. One specimen, Station 2252, Ngarumaoa Island, Raroia Atoll, Tuamotu Archipelago; collected by Maxwell Doty, Sept. 3, 1952.

DISCUSSION: It has been necessary to apply a new name to this species, which was named when the genus was called *Crangon* instead of *Alpheus*, because of Krøyer's use of *Crangon nanus* in 1842 for a species no longer in *Crangon* (or *Crago*) in 1953. The new name is from the Hawaiian, and means "confusion" or "mixed-up mess."

This group of specimens presents three points worthy of discussion. First, while the chelae on all of the females are like those described from Hawaii, the three males in the collection, all between 10 and 11.5 mm. in length, present an overgrowth of the fingers of the large and small chelae similar to that reported below for *A. paragracilis* Coutière. In the large chela the dactylus is very elongate, acute, and curved; the fingers occupy a large proportion of the length of the chela. The inferior internal margin of the merus only bears two feeble spinules, fewer than those reported in specimens in the Marianas and

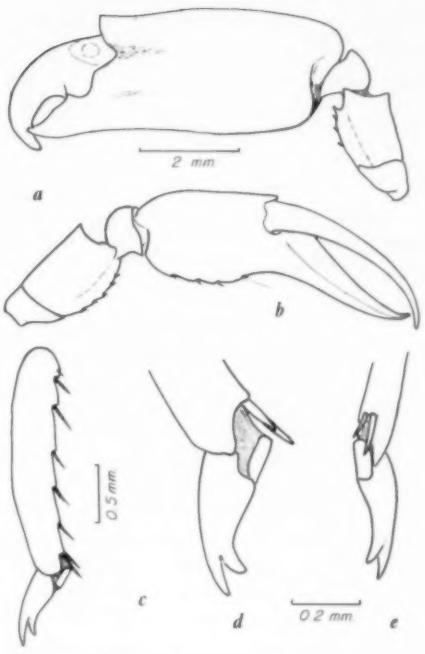


FIG. 5. *Alpheus huikau* nom. nov. *a*, *b*, Large and small chelipeds, showing overgrowth of fingers; *c*, third leg, merus and dactylus, anterior or medial aspect; *d*, *e*, third leg, dactylus, posterior and inferior aspects.

Arno. The small chela of the males also has the fingers elongate and curved; the merus is armed with two strong spines and three weaker spinules; the inferior margin of the palm bears two strong spines and two weaker spines, a characteristic not observed in previous specimens. This development of the chelae in the largest specimens is similar to that found for *A. paragracilis*. Unfortunately, neither this series of specimens, nor those from other islands, present a picture of gradual development as is found for *A. paragracilis;* however, a few other larger males, like those from Arno, do have a tendency towards the longer dactyli.

Second, is the peculiar development of an extra chitinized piece proximal to the dactylus and inferior to the distal end of the merus of

the third to fifth legs. This piece is borne by the tendon that reaches to the "heel" of the dactylus and is ordinarily obscured by the spines at the end of the dactylus if the animal dies with the dactyl straight or flexed towards the propodus. In many of these specimens, however, the dactylus was bent back on the propodus in death, so that the extra plate is apparent. The extra piece fits into an emargination of the inferior distal end of the propodus when the dactylus is straight or flexed. Other specimens of this species were re-examined and it was found that this development was carried by specimens from all areas studied. Moreover, specimens of the closely related *A. paragracilis* were also found to have the same structure.

Third, the outer uropods of these specimens bear several broad teeth on the distal articulation, and the inner uropod on its outer distal margin bears several small spines; neither of these characteristics was found in the specimens from Hawaii. This difference is not considered worthy of taxonomic emphasis.

The single specimen from the Tuamotus differs from the Hawaiian specimens in two minor ways. First, the rostrum is slightly shorter instead of slightly longer than the orbital hoods; second, the third and fourth carpal articles of the second legs are 1.3 and 2.0 times as long as broad instead of being broader than long. This latter characteristic may be important, but one specimen is not adequate for drawing such a conclusion.

Alpheus paragracilis Coutière
Fig. 6*a–d*

For synonymy, see Banner, Pacific Sci. 10(3): 345, 1956.

LOCALITIES: 1 specimen, Station Y-252, Yap Island, Caroline Archipelago, under small rocks on outer reef; collected by R. W. Hiatt, 1946. Nine specimens, Midway Island, Hawaiian Archipelago; collected by Y. Speicer, 1941.

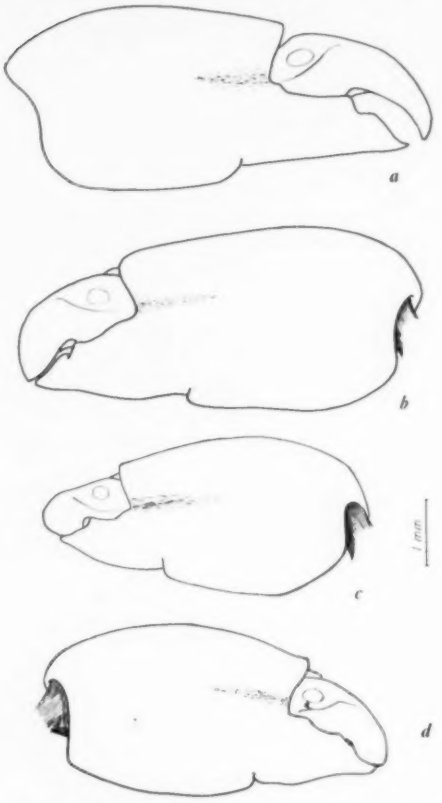


FIG. 6. *Alpheus paragracilis* Coutière, variation in the large chela. *a*, Male, 11.4 mm. long; *b*, male 10.8 mm. long; *c*, female, 11.4 mm. long; *d*, male, 9.6 mm. long. All drawn to the same scale.

DISCUSSION: These specimens present an interesting series on the change of form of the large chela with growth. The smaller males, less than 9.0 mm. long, and the females of all sizes have similar chelae, about twice as long as broad, and about 3.5 times the length of the fingers; the fingers of the dactylus are short, heavy, and rounded distally. However, on the largest male in the collection, 11.4 mm. long, the chela is 2.4 times as long as broad, and only 2.3 times the length of the fingers, and the dactylus is long, thin, curved and acute on the end. Between these two condi-

tions are found intermediate males, progressing from rounded condition of the immature forms to the acute form of the oldest male. It is also noteworthy that the chelae in the males are 1.5 times the length of those of the females of the same size.

In other collections examined and reported upon in previous papers, including those from Hawaii, this condition was not seen.

Alpheus macrochirus Richters

For synonymy, see Banner, Pacific Sci. 11(2): 198, 1957.

LOCALITIES: 2 specimens, Washington Island, Line Islands, in coral, Whippoorwill Expedition; collected by C. H. Edmondson, August, 1924.

Alpheus edmondsoni (Banner)

Crangon edmondsoni Banner, Pacific Sci. 7(1): 78, fig. 26, 1953.

LOCALITY: 1 specimen, Station 2063, Oneroa Island, Caroline Archipelago, from surge channel, on outer reef beyond *Lithothanmion* ridge; collected by Morris, Doty, and Herre, August 6, 1952. (Specimen without chelae, therefore identification questionable.)

Alpheus ventrosus Milne-Edwards

For synonymy, see Banner, Pacific Sci. 10(3): 345, 1956.

LOCALITIES: 2 specimens, Station Y-214, Tomil Harbor, Yap Island, Caroline Archipelago, in *Pocillopora* at 3.0 feet; collected by R. W. Hiatt, 1946. Eight specimens from racimose coral heads east side Tomil Harbor, Station Y-215; other data as above. Two specimens from Kaneohe Bay, Oahu, Hawaiian Archipelago; collected by A. H. Banner, August 24, 1955.

DISCUSSION: The pair of specimens, male and female, from Hawaii are included in this paper because of their unusual color pattern. Wherever I have collected this species in the Pacific the color has been the same, a basic orange red, with spots and sometimes stripes of deeper red. This pair, from the same head of *Pocillopora meandrina* var. *nobilis* Verrill, had in life a ground color of white with a tinge of pinkish yellow, and carried a series of paired irregular dark reddish-brown spots on either side of the middorsal line, three pairs on the carapace, and one pair on each abdominal somite. Similar but smaller spots were found at the bases of the abdominal pleura. Only the large and small chelae had the color usually characteristic of this species. The female carried larvae, recently hatched but still clinging to the pleopods, of pale violet color. No morphological differences were found between these and the normally colored specimens.

Obesomanus Group

Alpheus lutini Coutière

For synonymy, see Banner, Pacific Sci. 10(3): 346, 1956.

LOCALITIES: 1 specimen at Y-214, 2 at Y-215, collection data as in *A. ventrosus* above.

Alpheus phyrgianus Coutière

For synonymy, see Banner, Pacific Sci. 10(3): 346, 1956.

LOCALITY: 1 specimen from Palmyra Island, Line Islands, in coral; collected by C. H. Edmondson on Whippoorwill *A* Expedition, August, 1924.

Crinitus Group

Alpheus frontalis H. Milne-Edwards

For synonymy, see Banner, Pacific Sci. 10(3): 357, 1956.

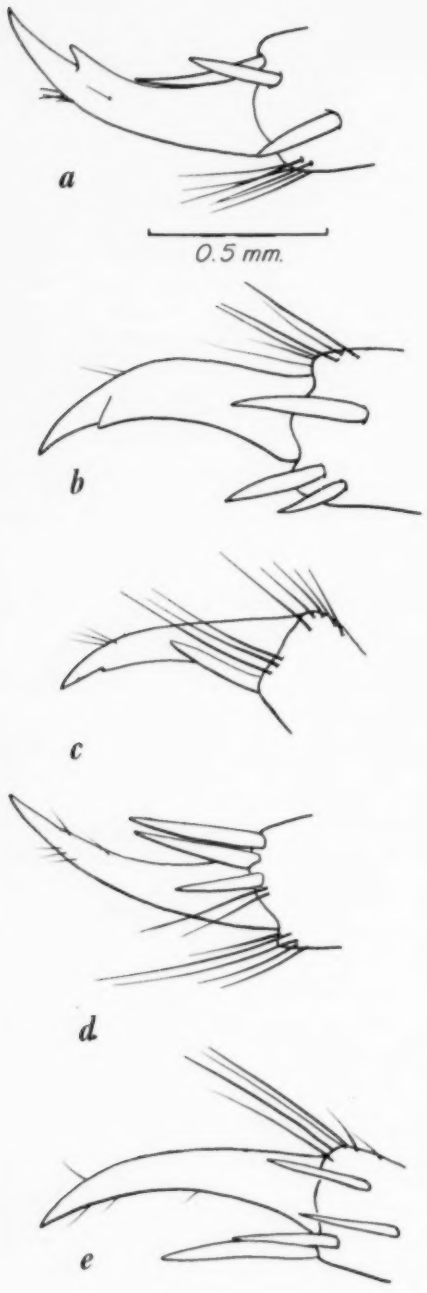
LOCALITY: 2 specimens, Station 1963 from Hamahomo Island, Tuamotu Archipelago, in algal tubes, under rocks, near shore; collected by J. E. P. Morrison, July 21, 1952.

Diadema Group

Alpheus diadema Dana

Fig. 7*a–e*

For synonymy, see Banner, Pacific Sci. 10(3): 357, 1956.



LOCALITIES: 2 specimens, Midway Island, Hawaiian Archipelago; collected by Y. D. P. Speicer, 1941. Six specimens, Ahoolaka ("Sand Island"), Kaneohe Bay, Oahu, Hawaiian Archipelago, under coral heads; collected by A. H. Banner, August, 1955.

DISCUSSION: In the group of specimens from Kaneohe Bay listed above an interesting variation occurs in the dactyli of the third, and to a lesser extent, the fourth legs. In most of the specimens from Hawaii these dactyli are either simple like the neotype (Banner, 1953, fig. 43j) or with a very small thickening or shoulder similar to those shown in Figure 7*c*, *d*. However, in this group of specimens from Kaneohe Bay, three specimens, male and female, have a definite and well-developed secondary unguis (Fig. 7*a*); the other specimens from the same locality had the secondary unguis developed as a shoulder only (Fig. 7*b*). There are no other noteworthy variations in either group of specimens. In the whole series of specimens it is the third legs that have the greatest development of the secondary unguis, and usually the fourth have but a slight thickening at most; moreover, often the accessory tooth or shoulder is not of uniform bilateral development.

The extensive collections of this species from the central Pacific area were spot checked for this characteristic, and it was found that most specimens were of intermediate development, similar to the conditions shown in Figure 7*b–d*. The extreme development, similar to the conditions shown in Figure 7*a* and *e*, were both rare.

Obviously, no significance should be attached to this variation.

An error in the redescription (Banner, 1953: 119) should be corrected. In describing the dactylus of the third legs, the text states: "Dactylus simple . . . as long as merus." In-

FIG. 7. *Alpheus diadema* Dana, variation in the dactyli of the third legs. *a*, Male, 19 mm. long, Kaneohe Bay, Hawaii; *b*, female, 24 mm. long, same locality; *c*, male, 15.5 mm. long, Tutuila, American Samoa; *d*, male, 18 mm. long, Midway Island; *e*, male, 17 mm. long, Tongatabu, Tonga. All drawn to the same scale.

stead, it should read: "Dactylus simple . . . as long as merus is broad."

Alpheus lanceloti Coutière
Fig. 8*a–k*

For synonymy, see Banner: 1958: 167.

LOCALITIES: 13 specimens, some ovigerous; Ahoolaka ("Sand Island") Kaneohe Bay, Oahu, Hawaii; collected from silty sand flats at tide level by A. H. Banner. Maximum length about 20 mm.

DISCUSSION: These specimens agree well with the original description by Coutière on the general configuration and most details; there are, however, some differences. The rostral front in general agrees with Coutière's description and figures (1905*a*: 900, pl. 63, fig. 39) but some variation occurs: the rostrum may be slightly longer, the rounded rostral ridge may not reach any further back than the middle of the orbital hoods, the frontal margin at either side of the rostrum may be definitely concave instead of almost straight, and finally the line or ridge at the inner margin of the orbital hoods is usually lacking. ("Le rostre est . . . séparé des voûtes orbitaires par un sillion. . . .") Slight and variable differences are similarly found in the proportions of the antennular peduncle and thoracic legs. In the large chela, as in the specimen already reported from Onotoa, the merus bears movable spines instead of teeth as shown by Coutière; moreover, the ischium of the same appendage bears three or four movable spines. The greatest difference is in the small chela of the male, which Coutière shows to be slender, with the fingers equalling the palm in length, while in these specimens the fingers are 1.2 times as long as the palm, slightly expanded in the middle, hooked on the end, and bear a fringe of setae, similar to a "balaeniceps-form," except that it does not cross over the superior face of the chela. The small chela of the females and immature males is similar to that drawn by Coutière. Coutière may have overlooked the sexual dimorphism. The small chela of the male from Onotoa was similar to the form described by Coutière. It should be noted that the large chela is laterally compressed, approaching the condition found in the Rapax group, but twisted, so that in these figures, and presumably those of Coutière, the compression is not shown.

In life the specimens had a basic light "sandy color," similar in hue to their environment; the chromatophores on their abdomens were in irregular and imperfectly defined bands. Their eggs were bright green.

These specimens were found burrowing into the coherent fine sand of a broad sand flat. While their burrows were not traced, from the depths of the excavations necessary to capture the shrimp it is estimated that they penetrate into the sand about 12–15 inches. In the same environment, but burrowing more deeply, are found *A. rapax* (Fabricius) and a callianassid shrimp.

The figures are included to complete the series of figures of Hawaiian species.

Brevirostris Group

Alpheus rapax Fabricius
Figs. 9*a–d*, 10*b*

For synonymy, see Banner, Pacific Sci. 10(3): 358, 1956.

LOCALITIES: About 40 specimens, Kaneohe Bay, Oahu, in shallow burrows on the inshore mud flats, intertidal zone; two specimens from deep sand burrows on Ahoolaka ("Sand Island") low in the intertidal zone, Kaneohe Bay, Oahu, Hawaii; collected by A. H. Banner, 1955, 1956.

DISCUSSION: These specimens seem to be of two different size ranges according to their habitats; those from the shallow burrows (possibly up to 6 inches deep in the mud flats, with *A. platyunguiculatus* (Banner) occupying deeper burrows reaching into buried coral heads) were mature individuals with the carapace lengths up to 7.6 mm., while the two from the deep burrows in the fine sand of Ahoolaka were found from 12 to 18 inches down (with *A. lanceoloti* Coutière in shallow

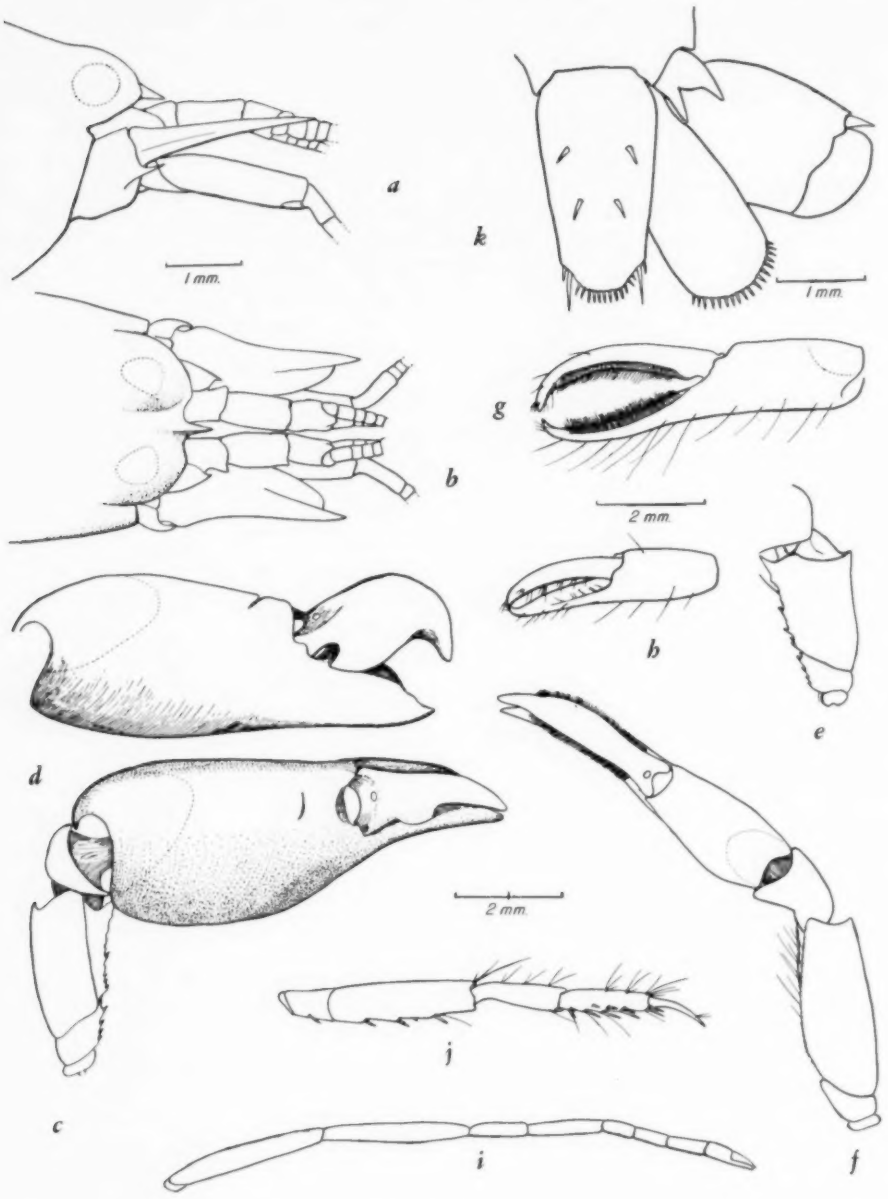


FIG. 8. *Alpheus lanceloti* Coutière. *a*, *b*, Anterior regions, dorsal and lateral aspects; *c*, large cheliped; *d*, large chela, inferior aspect; *e*, large cheliped, merus, medial aspect; *f*, small cheliped, male; *g*, small chela, male, inferior aspect; *h*, small chela, female; *i*, second leg; *j*, third leg; *k*, telson and uropods.

burrows) and were almost twice that size (carapace length of 13.5 mm., total length to 32 mm.). Because of this difference in size and habitat the individuals were carefully studied to see if any specific differences occurred between them. The large specimens were found to fall well within the range of variation of the small specimens. The difference in size may be due to the difference in habitat. The difference in the depth of burrows may be due to the underlying substrate of coral in the mud flats which prevents them from excavating their burrows as deeply as they can in the pure sand of the bar.

The variation in a group of 30 specimens, including the 2 large specimens, was tabulated with the following results.

Antennular peduncle: Second article from 1.4 to 2.5 times the length of the first. Third article from 0.6 to 1.1 times the length of the first.

Scaphocerite: Usually slightly to definitely longer than both carpocerite and antennular peduncle.

Carpocerite: Usually equal or subequal in length to the antennular peduncle; in two specimens, otherwise normal, equal in length to the scaphocerite, definitely longer than antennular peduncle.

Large chela: Total length usually 1.5 to 1.8 times breadth. Fingers usually 0.4 to 0.7 length of palm.

Small chela: Palm 1.2 to 1.5 usually 1.4, times as long as broad in males, 1.1 to 1.8, usually 1.3, times as long as broad in females.[3] Fingers 1.5 to 1.8, usually 1.7–1.8, times the length of palm in males, 1.4 to 1.8, usually 1.4–1.6, times length of palm in females.

Carpus, second legs: Second article 0.7 to 1.0 times length of first article, with most 0.8 times.

In one specimen a very peculiar large and small chela was noted. In this specimen the fingers of the large chela were 1.1 times the length of the palm, and the small chela was much thinner than usual, and not *balaeniceps*-shaped as would be expected for a male. (Fig. 9*c–d* contrasts these chelae with normal male chelae of approximately the same size.) All other characteristics are like those of the typical *A. rapax*. A similar condition has been previously reported. De Haan (1850: 178, pl. 45, fig. 4) described a new species, *A. digitalis*, separated from *A. rapax* only by the great elongation of the dactylus of the large chela. Coutière (1898*b*:248) examined the type of this species and two other species of the genus described on the basis of similar characteristics, and came to the conclusion that these were examples of regeneration where the development was arrested "à un stade

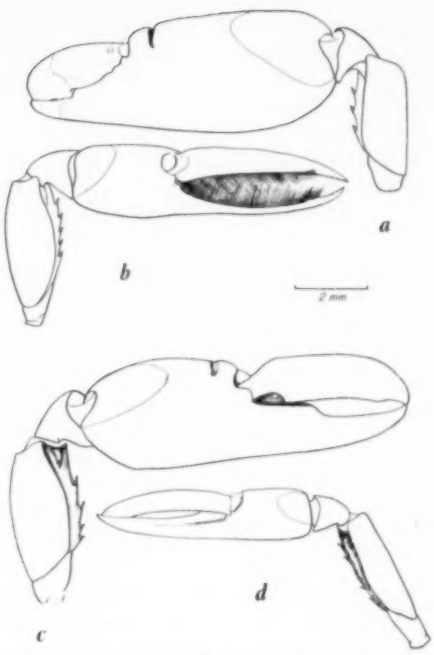


FIG. 9. *Alpheus rapax* Fabricius. Aberrant large and small chelae. *a*, *b*, Normal large and small chelae of male; *c*, *d*, aberrant large and small chelae, male. All drawn to same scale.

[3] In my original description of the Hawaiian specimens (1953: 128, top line, left column) there is an error for the palm was 1.5, not 2.5, times as long as broad.

moins profondément 'évolué' que sa forme habituelle," and that *A. digitalis* was a synonym of *A. rapax*. I believe a more logical explanation of this condition may be found in the process of either the normal replacement of a lost large chela, or the rather unusual replacement of both chelae. In the normal replacement of the large chela during successive molts, the small chela grows larger and takes on the appearance of the small chela; the condition drawn may be an intermediate stage where the small chela is regenerated, and the growing large chela has its size but not its final characteristics. In the replacement of both chelae, Darby (1934: 349, *et seq.*) reported that if the timing of loss of the individual appendages was controlled, they were replaced not by normal large and small chelae but by chelae of "intermediate" development.

Finally, many, but not all, of these specimens have the inferior external margin of the merus of the small cheliped bearing extremely fine and irregular movable spines or serrations; under ordinary magnification these are not noticeable, and even under 100 diameters of magnification it could not be discerned whether these projections were articulated. This, too, was not found in the regenerating chela mentioned above.

FIG. 10. *Alpheus platyunguiculatus* (Banner) and *Alpheus rapax* Fabricius, third maxillipeds, medial aspects. *a*, *A. platyunguiculatus; b*, *A. rapax*. Drawn to to the same scale.

Alpheus platyunguiculatus (Banner)
Fig. 10*a*

Crangon platyunguiculata Banner, Pacific Sci. 7(1): 130, fig. 47, 1953.

LOCALITIES: 8 specimens, the largest a 34 mm. ovigerous female, all collected from silt-buried coral heads in the intertidal mud flats behind the shoreward reefs of Kaneohe Bay, Oahu, Hawaii. Collected by A. H. Banner.

DISCUSSION: Since the collection of the five specimens upon which the original description was based, continuing search has been made for more specimens of this species. As explained in the original description, these shrimp appear to be confined to burrows in the muddy to sandy areas where the burrows can reach down through the loose substrate into buried coral heads. A section of inshore reef was found where the buried coral was loose and breakable; in this area these specimens were found, together with *A. rapax* (Fabricius). When only shallow holes were dug, several inches deep to the top of the imbedded coral, only *A. rapax* was found; when the imbedded coral itself was broken up from a depth of 8 inches or a foot, both *A. platyunguiculatus* and *A. rapax* were found. It appeared that the *A. rapax* was probably carried down from the sides of the excavation.

In the examination of these specimens an excellent specific characteristic was found to separate this species from *A. rapax*. In *A. platyunguiculatus* the middle article of the 3rd maxilliped bears a dense tuft of hairs, the longest reaching about one-third the length

of the ultimate article (Fig. 10*a*); in *A. rapax* this article bears a smaller group, not a tuft, of hairs, the longest of which reaches to the end of the ultimate article. In a few specimens of *A. platyunguiculatus* the tuft is not fully developed, but all lack the long setae of *A. rapax*.

Alpheus platyunguiculatus was separated from related species, especially from *A. sauvensis* de Man, on the basis of a series of minor differences in the proportions of the appendages.[4] This series of specimens was closely examined in those points of distinction, the results of which are given below:

	TYPE SPECIMEN	RANGE OF THIS SERIES
Ratio of lengths of first two antennular articles	1:1.3	1:1.4–1:2.0
Large cheliped		
Merus, length ÷ breadth	2.5	2.2–2.8
Number of meral spines	2	2–5
Chela, length ÷ breadth	2.3	2.1–2.6
Chela, finger length ÷ palmar length	0.5	0.4–0.7
Small Cheliped		
Merus, length ÷ breadth	2.6	2.0–2.8
Spines	4	2–5
Chela		
Palm, length ÷ breadth	1.5 female 1.6 female	1.5 sole male 1.3–1.6 females
Finger length ÷ palmar length	1.2 male 1.2 female	1.25 male 1.25–1.50 females
Second legs, ratio of first two carpal articles	1:2.3	1:1.85–2.3
Third legs		
Merus, length ÷ breadth	4.0	4.3–5.0

This range of variation destroys the value of most of the criteria set forth for the separation of *A. sauvensis* and *A. platyunguiculatus;* it also casts some doubts on the value of couplets used in de Man's key to this group. However, de Man (1908:110) specified that the dactyls of the third to fifth legs in his species were simple and rounded, and in all these specimens they are definitely flattened. Moreover, de Man did not describe the tuft of dense hairs on the penultimate joint of the third maxillipeds, and he did describe the terminal setae of the last article of this appendage as being over twice as long as the article, while in this species they are not even as long as the article. I believe, therefore, that this species is valid.

[4] In the tabulation on p. 132 of the original description the reference to the stylocerite should be to the scaphocerite, and in the comparison to *A. djeddensis* in the paragraph preceding the tabulation the text should read "small chela" instead of "third chela."

Edwardsii Group

Alpheus bastardi Coutière

Alpheus bouvieri var. *bastardi* Coutière, Soc. Ent. de France, Bul., 1898(5): 133, fig. 1a, 1898.

Alpheus bastardi Coutière, Fauna and Geog., Maldive and Laccadive Archipelagoes 2(4): 907, pl. 85, fig. 45, 1905.

LOCALITIES: 1 specimen, Station Y-111, Tomil Harbor, Yap Island, Caroline Archipelago, from holes in intertidal zone, rocky beach; collected by R. W. Hiatt, 1946.

DISCUSSION: This single specimen, a female, agrees perfectly with the short description and figures of Courtière. Unfortunately there is no male with which to confirm the identification.

Alpheus crassimanus Heller

Fig. 11*a–e*

For synonymy, see Banner, Pacific Sci. 11(2): 204, 1957.

LOCALITIES: 3 specimens from Station Y-111, collection data as above. One specimen, Station 2015, Otikaheru Island, Tuamotu Archipelago, on coral stones, under surface of muddy sand, near shore of brakish enclosed lagoon; collected by J. E. P. Morrison, July 29, 1952.

DISCUSSION: Most of the previous studies on this species have indicated that the small chela of the male not only has the dactylus subspatulate and fringed with long setae, but also that the palm bears sculpturing (see de Man, 1911, p. 417; Bate, 1888: pl. 99, fig. 2;

Coutière 1899: fig. 293). Yet the illustrations showed slight differences in the sculpturing (contrast Bate, fig. 2k to Coutière, *loc. cit.*). In contrast, the specimens reported from Hawaii (Banner, 1953: 134) did not show the sculpturing, nor did those reported from Arno and Onotoa (Banner, 1957: 204; 1958: 168).

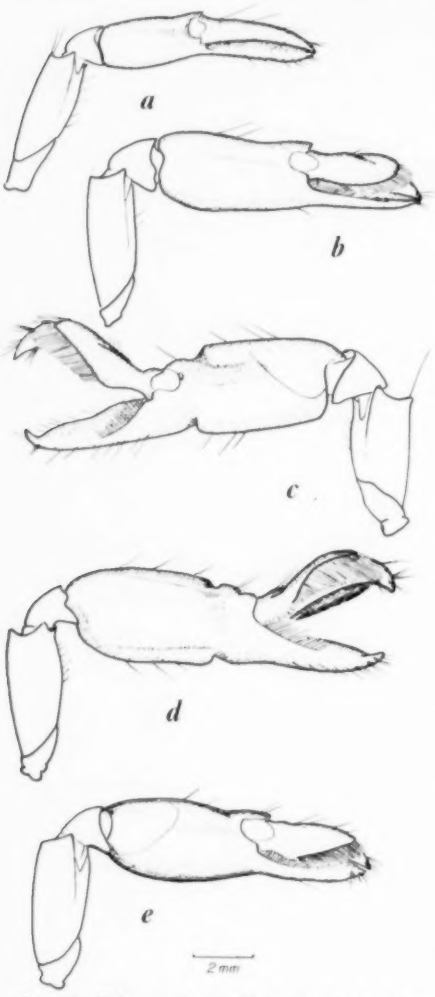


FIG. 11. *Alpheus crassimanus* Heller. Variation in form of small chelae. *a*, 22 mm. ovigerous female; *b*, 22 mm. male; *c*, 27 mm. male, lateral aspect; *d*, same, medial aspect; *e*, 24.6 mm. male. Specimens shown in *a–d* from Yap, *e*, from Hawaii; all drawn to same scale.

The three specimens from Yap indicate a possible reason for this difference. One of the specimens is an ovigerous 22 mm. female, which shows a slight trace of sculpturing in a shallow, ill-defined depression located longitudinally on the upper surface of the palm. The male of the same size has the characteristic dactylus of the adult male, yet the palm, like that of the female, bears only a slight longitudinal depression. However, in the 27 mm. male the palm is strongly sculptured. It is very roughly triangular in cross section, with the upper medial and lateral faces bearing extensive depressions that are quite well deliminated (although not as definite as the corresponding depressions on the large chela); these are connected across the superior margin by a rounded, saddlelike transverse groove. On the inferolateral margin there is a strong shoulder; the inferior surface of the chela is flattened and demarked by abrupt but rounded margins; the inferolateral shoulder does not continue on the inner face.

Specimens from Hawaii were re-examined, and while the smaller males show almost no trace of the sculpturing, the largest male available (24.6 mm. long, collected in the mud flats at Heeia, Kaneohe Bay, Oahu in about plus 1 to 2 ft. tide zone) shows sculpturing similar to that of the 22 mm. Yap specimen.

Inasmuch as specimens less than 20 mm. long are often ovigerous, and inasmuch as specimens up to 44 mm. long have been reported (de Man, 1902: 880), it appears that the younger, but mature, males bear the subspatulate dactylus but may be entirely lacking in the sculpturing of the palm, while larger males develop the sculpturing. It is likely that the point of transition between the two forms may be around the body length of 25 mm., although this size may vary in different geographic areas. For example, none from Hawaii appear to reach the necessary size, while the specimen reported by de Man from Makassar (*loc. cit.*) evidently had the sculpturing at a body length of 25 mm.

It may be that this is the wrong conclusion to draw from these specimens. Certainly two male specimens are not enough to prove or disprove the relationship. Only when a series of specimens of different body lengths are available can it be safely said that this is or is not a growth difference.

It should also be noted that the merus of the larger chelipeds of the 22 mm. female and the 27 mm. male bear a small acute tooth at the termination of the inferior internal margin, while the 22 mm. male, like those from Hawaii, lack this tooth.

The one specimen from the Tuamotus is a smaller male and similar in the form of the small chela to those from Hawaii.

Alpheus strenuus Dana

For synonymy, see Banner, Pacific Sci. 11(2): 204, 1957.

LOCALITY: 1 specimen, Station Y-122 from Tomil Harbor, Yap Island, Caroline Archipelago, in shallow burrows, intertidal zone; collected by R. W. Hiatt, 1946.

Alpheus pacificus Dana

For synonymy, see Banner, Pacific Sci. 10(3): 362, 1956.

LOCALITY: 2 specimens from Midway Island, Hawaiian Archipelago; collected by Y. D. P. Speicer, 1941.

Alpheus malabaricus (Fabricius) *mackayi* subsp. nov.

Fig. 12*a–n*

Astacus malabaricus Fabricius, System. Ent. p. 415, 1775.

Alpheus malabaricus Fabricius, Sup. Ent. System., p. 405, 1798.

Alpheus malabaricus Henderson, Zool. Soc. London, Trans., II, 5: 434, pl. 40, figs. 1–3, 1893. [Species reestablished and redescribed.]

Alpheus malabaricus de Man, Siboga Exped. 39a[1] (2): 429, 1911. [New subspecies with separate synonymy.]

Alpheus malabaricus Barnard, South African Mus., Ann., fig. 142 l-n, 1950.

Crangon species, McKay, Canad. Field-Nat. 61(4): 135, pl. 1, 1947.

TYPES: Holotype, an ovigerous female 37.8 mm. long; allotype, a male 27.7 mm. long; both collected by Donald C. G. MacKay in Wailupe fish pond, Oahu, Hawaii.

DESCRIPTION: Orbital hoods and rostrum protruding far beyond anterolateral margins of carapace. Orbital hoods inflated, high, rounded; rostrum short, not reaching beyond anterior margin of orbital hoods, carina short, rounded, not reaching to middle of orbital hoods; interorbital area behind termination of carina flat, anteriorly abruptly demarked from convexity of orbital hoods.

Antennular peduncle with second article about 2.4 times as long as broad, about twice length of visible portion of first article and not quite 3 times length of third article. First article terminating in high setose crest on superior margin; basicerite broad, flat, with small anterior tooth not reaching to end of first article. Basicerite with acute lateral tooth. Scaphocerite reaching to beyond end of antennular peduncle, squamous portion broad, slightly narrowing distally, and exceeded by the lateral spine; lateral spine curved inward at tip. Carpocerite reaching to end of lateral spine of scaphocerite.

Large chela of male and female of similar proportions, and almost identical size in spite of difference in body lengths. Merus with outer face 1.7 times as long as broad; superior margin ending distally in slight projection; inferior internal margin terminating in strong acute tooth, otherwise unarmed. Carpus of usual form. Large chela 2.4 times as long as maximum width, tapering towards fingers, with maximum width of fingers 0.66 as wide as palm; fingers strong, occupying the distal 0.3 of chela (about half as long as palm). Palm with rounded depressed areas on either face, both roughly triangular; superior margin of palm ending in shoulder overhanging shallow, rounded groove that connects de-

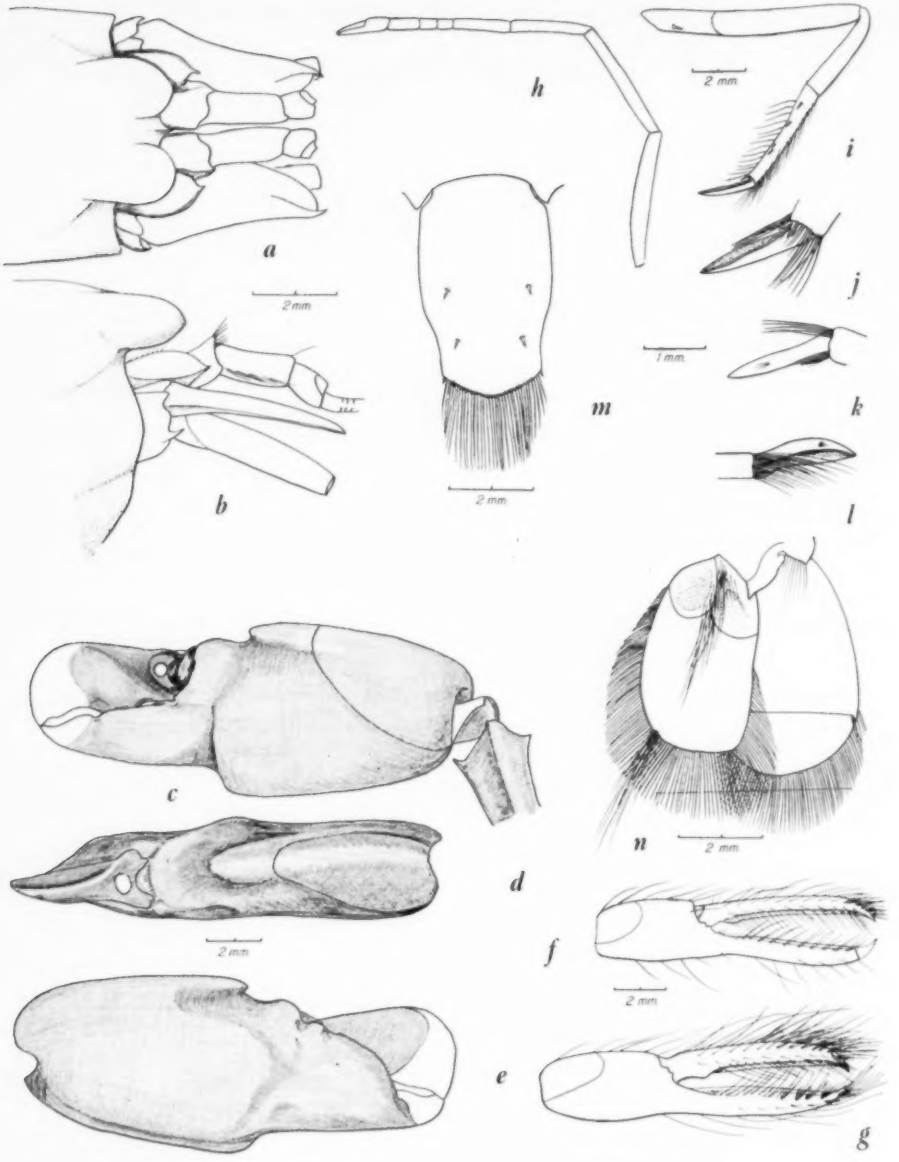


FIG. 12. *Alpheus malabaricus* (Fabricius) *mackayi* subsp. nov. *a*, *b*, Anterior regions, superior and lateral aspects, setae not shown; *c*, *d*, *e*, large chela, lateral, superior and medial aspects; *f*, small chela, male; *g*, small chela, female; *h*, second leg; *i*, third leg; *j*, *k*, *l*, dactylus, third leg, anterior, superior and posterior aspects; *m*, telson; *n*, uropod, showing proximal concavities.

pressed areas on either face; inferior margin terminating, almost right angled, in strong shoulder on outer face.

Small chelae also similar in both sexes. Merus unarmed on inferior internal margin. Palm slender, rounded, without sculpturing. Fingers 1.4 times length of palm in female, 1.7 times length of palm in male, straight except for slightly hooked tips, both movable and fixed fingers rounded on outer portion of opposing faces, bearing a sharp cutting edge on inner margin; dactylus bearing a low rounded tooth proximal to cutting edge.

Carpal articles of second legs with the ratio: 10:7.6:2.0:2.3:4.3; chela, in same ratio, 1.7.

Third and fourth legs with ischium bearing weak spine; merus 6 times as long as broad, unarmed; carpus 0.6 as long as merus, without distal teeth or projections; propodus 0.75 as long as merus, bearing 6 feeble spines and numerous long setae; dactylus 0.3 as long as merus, strongly curved in superior view, roughly triangular in cross section, with both superior faces somewhat convex, inferior face broad and flattened. Fifth leg with brush on propodus strongly developed.

Telson 2.4 times as long as posterior margin is broad, 1.3 times as broad anteriorly as posteriorly; in dorsal view, anterior 0.6 with slightly convex margins, without taper, then tapering abruptly to posterior portion with parallel margins; in lateral view, middle of lateral margin strongly depressed; tip strongly arcuate. Dorsal spinules feeble; inner pair of posterolateral spinules so slender that they can be confused with terminal setae; terminal setae numerous and heavy; posterior margin also armed with series of minute spinules. Outer uropod with spine on shoulder slight. Inner uropod with a shallow but well-demarked basin to accommodate depressed lateral margin of telson.

DISCUSSION: These specimens agree very well with the species *A. malabaricus* as redescribed by Henderson, and with the subspecies described by de Man (*loc. cit.*), except in the length of the rostrum and the relative proportions of the small chela; apparently all are similar in form of the dactylus of the third legs, in the general shape of the large chela, etc. However, all specimens of *A. malabaricus* except that described and figured by Barnard from South Africa (*loc. cit.*), have longer rostrums, and in none are the fingers as short when compared to the palm. Both reported subspecies have fingers on the small chela that are gaping instead of straight. The habitat of these specimens—the thick soft mud of a fish pond—and those reported by Henderson from India are also similar.

Because of their great similarities it is not logical to consider these specimens as other than a geographically isolated subspecies; it may be that when other specimens are found between Hawaii and India intergrading specimens will be found.

The type locality, Wailupe fish pond, no longer exists. It was filled in and is now used for homesites, the area being called Wailupe Peninsula. Presumably the subspecies exists elsewhere in the Hawaiian Islands, but it has not yet been found in other areas.

THUNOR Armstrong

Thunor microscaphis sp. nov.
Fig. 13*a–i*

Thunor sp. Banner, Pacific Sci. 10(3): 367, fig. 23a–e, 1956.

TYPE SPECIMEN: A 9.5 mm. male from Station 827, Likiep Atoll, Marshall Islands, USNM 194726; collected by S. V. MacNeil.

DESCRIPTION: Specimen with cephalothorax preponderant, abdomen reduced, only slightly more than equal in length to carapace.

Anterior carapace distorted in specimen with folds and wrinkles permitting the eyes to be partially exposed. Rostrum obtuse, short, not reaching beyond anterior margin of orbital hoods, and bearing low, rounded carina reaching to slightly past middle of orbital hoods. Orbital hoods large, inflated, evenly rounded anteriorly.

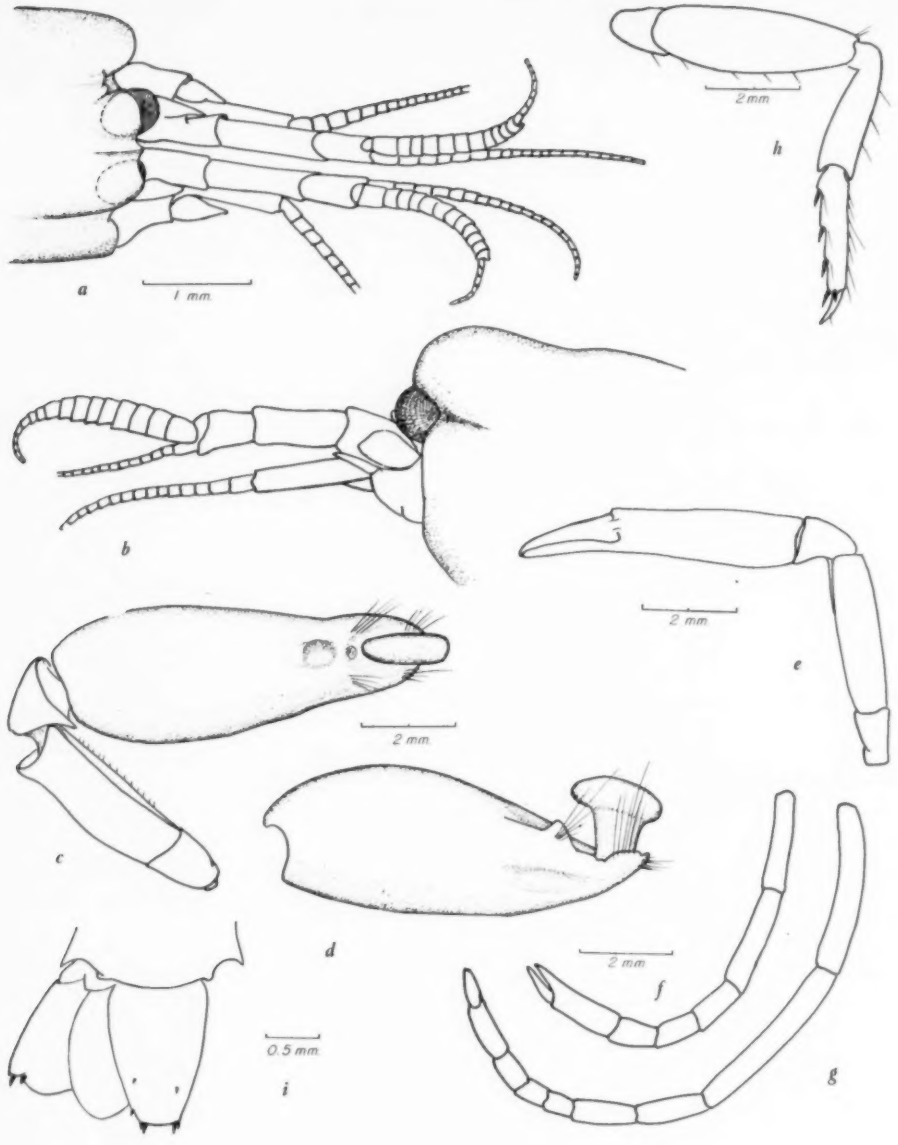


FIG. 13. *Thunor microscaphis* sp. nov. *a*, *b*, Anterior regions, superior and lateral aspects; *c*, *d*, large cheliped; *e*, small cheliped; *f*, second leg, left, carpus to dactylus; *g*, second leg, right, ischium to dactylus; *h*, third leg; *i*, telson and uropods.

Antennular peduncle with second article 1.7 times length of first article; third article subequal to first; second article 3.5 times as long as broad. Stylocerite assymetrically developed, with that on left almost rounded anteriorly and reaching about 0.7 the length of first article; that on right anterior irregular (but rounded) reaching only a little more than 0.5 length of first article.

Scaphocerite reduced to bract which reaches on left to end, on right to slightly beyond end of first antennular article. Basicerite unarmed. Carpocerite reaching 0.6 length of second antennular article. Antennal flagellum elongate.

Large chela 2.7 times as long as broad, with fingers occupying the distal 0.2; margins mostly regular and strongly tapering. Distally chela with a deep pit proximal to articulation of dactylus to accommodate protruding margin of dactylus; lateral and proximal to articulation of dactylus is located a shallow depression with poorly defined margins. Fixed finger very short. Dactylus hammer-shaped, with distal margin swollen and rounded, proximal portion broad and thin. Carpus of usual form. Merus about 0.4 length of chela, with outer face 3.5 times as long as broad; distally unarmed; inferior internal and external margins sharp; inferior internal margin bearing 13 slight and feeble spines.

Small chela 5 times as long as broad, with the simple fingers occupying the distal 0.35. Merus 0.55 length of chela, 0.25 as long as broad, unarmed.

Second legs assymetrical, with left as long as body, and right a little over half as long. Carpal articles of right legs with ratio: 10:9:4:5:6; left leg with first article slightly shorter, relatively.

Third leg with ischium unarmed; merus unarmed, 3.2 times as long as broad; carpus with distal angles rounded; propodus bearing 3 single inferior spines and paired spines distally; dactylus simple and curved.

Outer uropod bearing a single lateral spine without articulation, inner unarmed. Telson 3.5 times as long as tip is broad, 1.8 times as broad anteriorly as posteriorly; sides slightly curved. Dorsal spines abnormal, with anterior left about 0.7 length posterior from articulation, posterior left located on margin; anterior right posterior to corresponding left, posterior right missing.

DISCUSSION: This single specimen appears to be of the same species as the two fragmentary specimens previously described but not named from Saipan (Banner, *loc. cit.*). A number of slight differences are found between the two forms: the length of the interorbital carina, the proportion of the articles of the antennular peduncle, the ratio of the carpal articles of the second leg (only one second leg remained on the two Saipan specimens), the armature of the propodus of the third legs, and the proportions and armature of the telson. These differences, most of them in parts that have been found to be variable in *T. idiocheles* (Courtière) and *T. rathbunae* (Schmitt), as well as in related species of the Obesomanus group of *Alpheus*, are probably without significance. Another difference between the two lies in the development of the antennal peduncle: in the male specimen from Saipan the scaphocerite reaches to the middle of the second article of the antennular peduncle, and the carpocerite reaches to the end of the same article, while in the female from Saipan the developement of these is shorter and more degenerate than that found in the male. As this male is similar to the Saipan female, the difference is obviously not sexual dimorphism, but may show the variability of the development of this appendage; however, the two Saipan specimens may be of different species. A final difference is found in the merus of the large chela, which in this specimen bears 13 feeble spines, and in the Saipan specimen bears a few bristles in corresponding locations. Opposed to these slight and seemingly insignificant differences are many and great similarities, as can best be seen by comparing the figures of the two forms.

This species plainly belongs to *Thunor* if

that genus is to be accepted, for it lacks the anal tubercles and the articulation of the outer uropod; in addition the specimens lack the ocular beak and in two of the three specimens the cardiac notch is lacking.

Within the genus, *T. microscaphis* is best distinguished from *T. idiocheles* by the form of the large chela, for in this species the dactylus is formed like a two-headed hammer, and the superior surface of the chela bears a marked depression to accommodate the superior projection of the dactylus when that article is flexed. In *T. idiocheles*, the dactylus of the large chela lacks this superior projection and there is no corresponding depression of the palm. From *T. rathbunae* this species is distinguished by the presence of a small rostrum as well as by the form of the large chela and the relatively greater length of the small chela.

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Botanical Novelties on the Island of Niihau, Hawaiian Islands
Hawaiian Plant Studies 25[1]

HAROLD ST. JOHN[2]

IN 1947 and again in 1949 the writer was so fortunate as to be able to make botanical explorations on the island of Niihau, a remote, high island of the principal group of Hawaiian Islands. A lengthy account of its flora is in preparation. It seems desirable now to put on record the new botanical discoveries made on that island or in connection with the investigation of its flora.

The holotypes of the new species are in the Bernice P. Bishop Museum, Honolulu, (BISH), unless otherwise specified.

GRAMINEAE

Panicum Heupueo sp. nov. (subgenus *Panicum*)

Fig. 1

NOM. VERN.: "heu pueo" (=fine hairs on the owl); also called, "hakonakona," perhaps in error, as that is the established name of *P. torridum* Gaud.

DIAGNOSIS HOLOTYPI: Breviter annuum erectum 16–34 cm. altum plerumque e basi unicauliferum sed supra basem culmis bifurcatis cum ramis subaequalibus, internodis superioribus villosis inferioribus glabris, internodis plantarum parvarum quam vaginam brevioribus sed plantarum magnarum ad bis longioribus quam vaginam, vaginis 15–29 mm. longis valde nervosis pustulato-albiciliatis, pilis 0.2–0.4 mm. longis, laminis 4–10 cm. longis 2–4 mm. latis planis linearibus acutis albo-villosis in ambis lateris, paniculis 2–8 cm. longis 5–30 mm. latis densis in culmis omnibus terminalibus in basi vaginatis, ramulis adscendentibus valde adpressis sed post florendis ramulis superioribus paene divergentibus, rhachide ad basim sparse piloso sed ad apicem scabro, ramulis scabris, spiculis 1.2–1.5 mm. longis elliptico-ovoideis acutis glabris pallidis scariosis viridi-nervosis, gluma prima 1.9 mm. longa 1.2 mm. lata 3-nervata lanceo-ovata, gluma secunda 1.7 mm. longa 1.4 mm. lata late elliptica acuta 7-nervata, lemma sterilis 1.8 mm. longa 1.1 mm. lata late elliptica acuta, palea sterilis 1.1 mm. longa 0.5 mm. lata elliptica membranacea in basi involuta, lemma fertilis 0.9–1 mm. longa 0.6 mm. lata ovata cartilaginea lucida alba deinde brunneo-plumbaginea indistincte 5-nervata concava marginibus involutis, palea subconcava clausa 3-nervata, antheris 0.4 mm. longis oblongis, stigma dendritica.

DESCRIPTION OF ALL SPECIMENS: Short-lived annual, erect, 10–53 cm. tall, mostly 1-stemmed from the base, but above it the culms repeatedly bifurcate, with subequal branches; internodes villous on upper part, glabrous on lower; on small plants the internodes shorter than the sheaths but on larger ones the internodes as long as twice the length of the sheaths; leaf sheaths 15–48 mm. long, strongly nerved, pustulate white villous;

[1] This is the twenty-fifth of a series of papers designed to present descriptions, revisions, and records of Hawaiian plants. The preceding papers have been published in B. P. Bishop Mus., Occ. Papers 10(4), 1933; 10(12), 1934; 11(14), 1935; 12(8), 1936; 14(8), 1938; 15(1), 1939; 15(2), 1939; 15(22), 1940; 15(28), 1940; 17(12), 1943; Calif. Acad. Sci., Proc. IV, 25(16), 1946; Torrey Bot. Club, Bul. 72: 22–30, 1945; Lloydia 7: 265–274, 1944; Pacific Sci. 1(1): 5–20, 1947; Brittonia 6(4): 431–499, 1949; Gray Herb., Contrib. 165: 39–42, 1947; Pacific Sci. 3(4): 296–301, 1949; 4(4): 339–345, 1950; B. P. Bishop Mus., Occ. Papers 20(6), 1950; Pacific Sci. 6(1): 30–34, 1952; 6(3): 213–255, 1952; 8(2): 140–146, 1954; Polynesian Soc., Jour. 63(1): 27–34, 1954; B. P. Bishop Mus., Occ. Papers 21(15), 1955; Brussels Jard. Bot. de l'État Bul. 27(1): 49–54, fig. 2, 1957.

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FIG. 1. *Panicum Heupuco*, from the holotype: *a*, habit × 1; *b*, blade and sheath × 10; *c*, spikelet × 20; *d*, spikelet × 20; *e*, floret × 20; *f*, first glume, dorsal view, × 20; *g*, second glume, dorsal view, × 20; *h*, sterile lemma, dorsal view, × 20; *i*, sterile palea, ventral view, × 20.

ligule a narrow membrane, pilosulous ciliate with hairs 0.2–0.4 mm. long; blades 3–13 cm. long, 2–6 mm. wide, flat, linear, acute, white villous on both sides; panicles 2–15 cm. long, 3–50 mm. wide, dense, terminal on all branches, enfolded at base by the leaf blade or sheath, the ascending branches closely appressed, but after anthesis the upper ones slightly diverging; the rhachis sparsely pilosulous towards the base, but towards the apex scabrous; branchlets scabrous; spikelets 1.2–1.5 mm. long, elliptic ovoid, acute, glabrous, pale scarious, with greenish nerves; first glume 1.9 mm. long, 1.2 mm. wide, 3-nerved, lance-ovate; second glume 1.7 mm. long, 1.4 mm. wide, broadly elliptic, acute, 7-nerved; sterile lemma 1.8 mm. long, 1.1 mm. wide, broadly elliptic, acute; sterile palea present, 1.1 mm. long, 0.5 mm. wide, elliptic, membranous, enfolded at base; fertile lemma 0.9–1 mm. long, 0.6 mm. wide, ovate, cartilaginous, shining, white, then brownish lead-colored, faintly 5-nerved, concave, the margins inrolled; palea gently concave, enclosed, 3-nerved; anthers 0.4 mm. long, oblong; stigma dendritic.

HOLOTYPUS: Niihau, Kii, between basalt rocks, on rocky knoll, 100 ft. alt., April 2, 1949, *H. St. John 23,666* (BISH).

SPECIMENS EXAMINED: Kii, with same data, *St. John 23,665; 23,670.*

The new species is a member of the subgenus *Panicum* (formerly *Eupanicum*) but it is not here assigned to a section. Neither the treatment of the genus in North America by Hitchcock and Chase nor the world treatment by Pilger in the second edition of Engler's "Pflanzenfamilien" has any section into which this species will fit. It comes closest to agreeing with the characters of section *Capillaria*, but it disagrees in several characters.

The most closely related species is *P. Fauriei* Hitchc. of the islands of Hawaii, Maui, Molokai, and Oahu. This species differs in having the sheaths appressed puberulous, the ligule a membrane with pilose hairs 1 mm. long; the blades 0.8–3.5 mm. wide, mostly involute, and below appressed puberulous; the panicle rhachis and branchlets ascending villosulous; the spikelets 1.8–2.1 mm. long, and the fertile lemma 1.2 mm. long. In contrast, *P. Heupueo* is distinguished by having the sheaths villous; the ligule a very narrow membrane pilosulous ciliate with hairs 0.2–0.4 mm. long; blades 2–6 mm. wide, flat, villous above and below; panicle with the rhachis below sparsely pilosulous, above scabrous, the branchlets scabrous; the spikelets 1.2–1.5 mm. long; and the fertile lemma 0.9 mm. long.

Panicum radiatius nom. nov.

Paspalidium radiatum Vickery, N. S. Wales Natl. Herb., Contr. 1(6): 332–334, 1950; non *Panicum radiatum* R. Br., Prodr. Fl. Nov. Holl. 192, 1810 which is *Digitaria tonsa* D. K. Hughes, Kew Bul. 313, 1923.

The genus *Paspalidium* was described in the *Flora of Tropical Africa*, vol. 9, by Stapf. It was published in 1917 in the key only, then in 1920 a description of the genus and of the two species followed. The genus was validly published, but not contrasted with the related genera or discussed. It now has been accepted and enlarged, especially in Australia, but little has been added to substantiate its generic status. The spikelets are biseriate on 1-sided lateral spikes, but in detail are like those of species in the enormous genus *Panicum*. A revision of the Australian species has been announced by S. T. Blake, so a disposition of the other species should await that treatment. However, the structure of the spikelet agrees well with that of *Panicum* and the inflorescence seems to show a reduced state derived from a panicle, so it is here maintained that the best assignment for the species introduced to Hawaii is in the genus *Panicum*. A new name is proposed because of the existence of an earlier homonym in *Panicum*.

Niihau: Short grass that appeared on its own on Niihau, November 1, 1939, *G. C. Munro;* Kiekie, 50 ft. alt., cultivated pasture

grass, *St. John 23,661*. The Munro collection had once been determined as *Paspalidium caespitosum* C. E. Hubbard.

CYPERACEAE

Eleocharis calva Torr. var. ***australis*** (Nees) comb. nov.

Fig. 2

E. palustris (L.) R. & S. var. *australis* Nees, Acad. Caes. Leop. Nat. Cur., Nov. Act. 19, Suppl. 1: 96, 1843 (as *E. palustris* R. Br. β *Australis* Nees).

Scirpus nudissimus Steud., Soc. Linn. de Normandie, Bull. II, 9: 280, 1875, synon. nov.

E. palustris sensu Hbd., Fl. Haw. Is. 474, 1888, and of C. N. Forbes, B. P. Bishop Mus., Occ. Papers 7(5): 48, 1920; not of (L.) R. & S.

E. calva sensu Fernald & Brackett as to Oahu plant, Rhodora 31: 68–70, 1929; not of Torr.

E. macrostachya sensu Svenson as to Oahu plants, Rhodora 41: 57, 1939; not of Britt.

NOM. VERN.: "kohekohe."

Niihau: Loe Lake, 2 miles N. of Puuwai, marshy border of temporary flood-water lake, 10 ft. alt., plants up to 12 dm. tall, basal sheaths red, *St. John 23,598*.

Hillebrand (1888: 474) apparently did not encounter this plant in the Hawaiian Islands, but included it doubtfully in his *Flora of the Hawaiian Islands*, upon the report of Meyen's collection by Kunth (1843: 96). It seems strange that Hillebrand did not find this species. Quite a number of collections of it are now known and some of them were previous to Hillebrand's time in the Islands (1850–71). The collections are as follows:

1825: James Macrae (Herb. Lindley)

1831: Maio, in Oahu insula, F. J. F. Meyen (Vienna Herb.)

1842: Oahu, U. S. Exploring Expedition (Gray Herb.)

1920: Oahu, Kaimuki, creeping in the mud, March 26, 1916, *C. N. Forbes 2360.0* (Bishop Mus.)

1927: Oahu, *O. Degener 9,002* (N. Y.)

1949: Niihau, Puuwai, *H. St. John 23,598* (Bishop Mus.)

1950: Niihau, "tohetohe," September, *Henry Judd* (Bishop Mus.)

In 1929 Fernald and Brackett (p. 68) identified this with *Eleocharis calva* Torr., occurring from Quebec to Alberta and Washington, south to Florida, Oklahoma, and Mexico, and also in Manchuria. It is close to this species because of the close, red sheaths, the linear-lanceoloid spikes with a single basal sterile scale. This primarily American species has the plant loosely stoloniferous to slightly caespitose; culms 1–6.5 dm. tall, 0.5–1.5 mm. in diameter; lower and median fertile scales 1.8–3 mm. long, oblong to ovate, reddish to pale brown; anthers 1.3–1.7 mm. long; achenes 1–1.4 mm. long, 0.7–1 mm. broad; style base 0.2–0.4 mm. broad at base, conical; perianth wanting or of 1–4 delicate bristles usually equaling or slightly exceeding the style base. The local *E. calva* var. *australis* has the plant short stoloniferous but densely caespitose in habit; culms 1–12 dm. tall, 1–3 mm. in diameter; lower and median fertile scales 3–4 mm. long, lance-ovate, castaneous between the hyaline margin and the pale midrib; anther 2 mm. long; achenes 1.7–1.9 mm. long, 1.2–1.3 mm. wide; style base 0.4–0.6 mm. wide, deltoid-ovoid; perianth of 4 stout bristles, retrorse barbellate and nearly or fully as long as the achene. The Hawaiian plant seems clearly separable from *E. calva*.

In 1939 Svenson in his monograph reduced *Scirpus nudissimus* Steud. He called it a "nomen subnudum" (Rhodora 41: 57, 1939) but there is no such designation in our present International Code. There is the term "nomen nudum" for names published without any description. Steudel's description was as follows:

"5. Le *S. nudissimus*, Steud., se compose d'une tige terminée par un épi grêle, d'ou son nom spécifique; mais Steudel ajoute: nisi forte *Eleocharis palustris*, var?" This original publication included two items of descrip-

FIG. 2. *Eleocharis calva* var. *australis*, from St. John 23,598: *a*, habit × ½; *b*, spike × 5; *c*, achene × 20; *d*, stamen × 5.

tion: spikelet slender; plant appearing like a variety of *Eleocharis palustris*. If this plant (see Fig. 2) is compared with *E. palustris* (see Rhodora 31: pl. 181, figs. 1–4), it will be seen that the spikelets are much more slender.

Svenson also refers to *E. macrostachya* the Oahu plant described from the collection by Meyen. This was published as: "E. palustris R. Br. (β Australis Nees squamis spicae acutiusculis albis tenuibus nervo medio pallide viridi litura cuspitato fusco cincto.).

In Oahu insula, Maio 1831, Meyen; ex eadem insula Macrae in Herb. Lindl."

Both *Scirpus nudissimus* Steud. and *Eleocharis palustris* var. *australis* were referred by Svenson to *E. macrostachya* Britt. This species, occurring from Illinois to British Columbia, south to Louisiana, California, and Michoacan, is recognizable by having culms compressed, soft, very flat after pressure; lowest sterile scales 2–3; achenes averaging 1 mm. wide; bristles 5–6 (or –8, or 0) very delicate, often overtopping the achene and style base, the teeth slender. On the other hand, the Hawaiian *E. palustris* var. *australis* has the culm terete, soft, little flattened under pressure; lowest sterile scale 1, encircling the base ¼ way; achenes 1.2–1.3 mm. wide; the 4 bristles stout, nearly or quite equalling the achene body, with stout retrorse teeth.

It is also related to *E. palustris* (L.) R. & S., and more closely to its var. *major* Sonder which occurs from Labrador to British Columbia and south to Pennsylvania, Iowa, Wyoming, and California. This var. *major* has the sheaths 3–30 cm. long, comparatively loose; culms 5–19 dm. tall; spikelets 0.7–2.6 cm. long, 2.5–7 mm. thick, lanceolate to ovoid, ⅓ as wide as long; basal scales 2–3; lower and median fertile scales 3.2–5.5 mm. long; bristles 4, slender, commonly reaching to the middle of the style base; style base lanceoloid-conic, much higher than broad. The Hawaiian var. *australis* has the sheaths 3–8 cm. long, close; culms 1–12 dm. tall; spikelets 1.3–1.7 mm. long, 2.5–3.5 mm. thick, narrowly linear-lanceoloid, ¼ as wide as long; basal scale 1; lower and median fertile scales 3–4 mm. long; the 4 bristles stout, nearly or quite equalling the achene; style base deltoid-ovoid, as wide as long. In any other group, this isolated Hawaiian kind, having significant characters that separate it in the keys from the American and Eurasian species, in this instance from *E. palustris*, *E. calva*, and *E. macrostachya*, and even by its truncate, indurate, apiculate sheaths from subseries Palustres, a natural conclusion would be that it too should be classed as a species. However, consideration should be given to the commentary on the subseries Palustres by the recent monographer of the genus, H. K. Svenson (1939: 55, 59).

In the eastern United States . . . the entities are clear; in Europe and in the western United States, the situation seems to be chaotic. The *Palustres*, chiefly of holarctic distribution, have probably spread out in post-glacial time, achieving a variation comparable with that of *Rubus* or *Crataegus*. In Western United States, with its natural barriers and diversified terrain, numerous intergrading geographical races have developed, the most noteworthy of which I have illustrated by drawings and photographs. It would be perfectly easy to describe more species in this group, adding to the plethora of intangible species, but I have made little or no change. In my mind, there is even some question whether more than a single good species of the *Palustris* group exists in northwestern Europe, and whether in Europe these are not environmental responses to sea-strand, meadow, and bog, which parallel the variation of *E. palustris* in western America. Although I have spent an inordinate amount of time on this group and have seen a vast amount of material, the problems do not appear to be close to solution. . . . The *Palustris* group appears to be equally complex in Asia. . . .

He gives many details of the variability or plasticity of *E. palustris* and its relatives in Europe.

Realizing these facts, it does not appear wise to give the Hawaiian *Eleocharis* specific rank, even though there is a name available

for transfer. The plant is related to *E. palustris*, but that natural group has the spikelet with 2–3 sterile basal scales. Since the Hawaiian plant has, like *E. calva*, the single basal scale, the similar linear-lanceoloid spikes, the similar shaped achene and style base, and prominent red basal sheaths, it appears to be most closely related to that species. The differences between the two are tabulated a few pages back. When evaluated, these morphological differences are of some significance, but in the subseries Palustres with its variable or merging taxa distributed well around the northern hemisphere, the best method of classification seems the ultraconservative. It is concluded that the Hawaiian plant is a local, endemic variety, allied to *E. calva*, and best placed as a variety of it. Hence, the combination for it as a variety of that species is here made.

Now that abundant and complete material of this plant from Oahu and Niihau is at hand, it is possible to tabulate its characters, and re-evaluate its distinctions. Knowing the high endemism in the Hawaiian flora (92 per cent or more), one could easily take the view that with any clear differences, this plant could well be classed as an endemic Hawaiian species. It was collected as early as 1825 when there were few adventives present. It has been collected five times since then. Though it is not common, it must be remembered that it is a lowland plant of fresh marshy habitats. Most of the collections on Oahu were in present or former cultivated lands—taro patches. It was thus a weed in the taro patch. Most weeds are adventives, but in wet cultivations the percentage of native plants persisting in the taro patch, cranberry bog, or rice paddy is much higher than in dry land agricultural fields. On Niihau it was not in agricultural land, but by the edge of a small lake on the coastal plain bordering the mountainous upland. Flood waters make a lake that may last for several months, then for the remainder of the year the spot is parched and completely dry and alkaline. There is no taro cultivation anywhere in the vicinity. From the habitat and the manner of its occurrence, it seemed to the collector to be a native plant on Niihau. It may also be a native of Oahu, persisting only in existing or former taro patches. On a small island like Oahu, with a large population depending on taro as the basic crop, nearly all natural fresh ponds and swamps were converted into taro patches. Also, almost every lowland alluvial spot to which irrigation water could be conducted, was made into a taro patch. Thus, even in aboriginal times, the swampy habitats, natural to *Eleocharis*, were converted to intensively cultivated taro patches. Since the discovery and westernization of the islands, these lands on Oahu have in part been used continually as taro patches, but in recent times more largely occupied for sugar cane plantations or for house lots. The *Eleocharis* is now rare on Oahu, but well preserved on Niihau, and visible there for a few months after heavy southerly winter rains.

It is also significant that the deep red basal sheaths were gathered by the native Hawaiians on Niihau and plaited to form ornamental geometrical patterns, mostly small triangles, near the border of the pliant, fine mats called "pawehe" to distinguish them from the pure white ones called "makaloa," made solely of the stems of *Cyperus laevigatus* and lacking the red, ornamental inlay. It appears that the "pawehe" mats were made only on Niihau. Aylmer F. Robinson wrote (in a letter of July 26, 1952), "I believe the art is very old, and indigenous, though right now I do not think of any proof of it." There are in the Bishop Museum several of these mats, but none of the older ones are definitely dated. One was probably made at least as long ago as early in the 19th century. Hence, from the early occurrence on Oahu and Niihau, from the artistic use in fine matting by the natives, and from its distinctive morphology, it is concluded that *Eleocharis calva* var. *australis* is a variety endemic to the Hawaiian Islands. Since it has not been illustrated, and since

most of the older collections are incomplete or immature, an illustration made from the Niihau collection, *St. John 23,598*, is included.

PALMAE

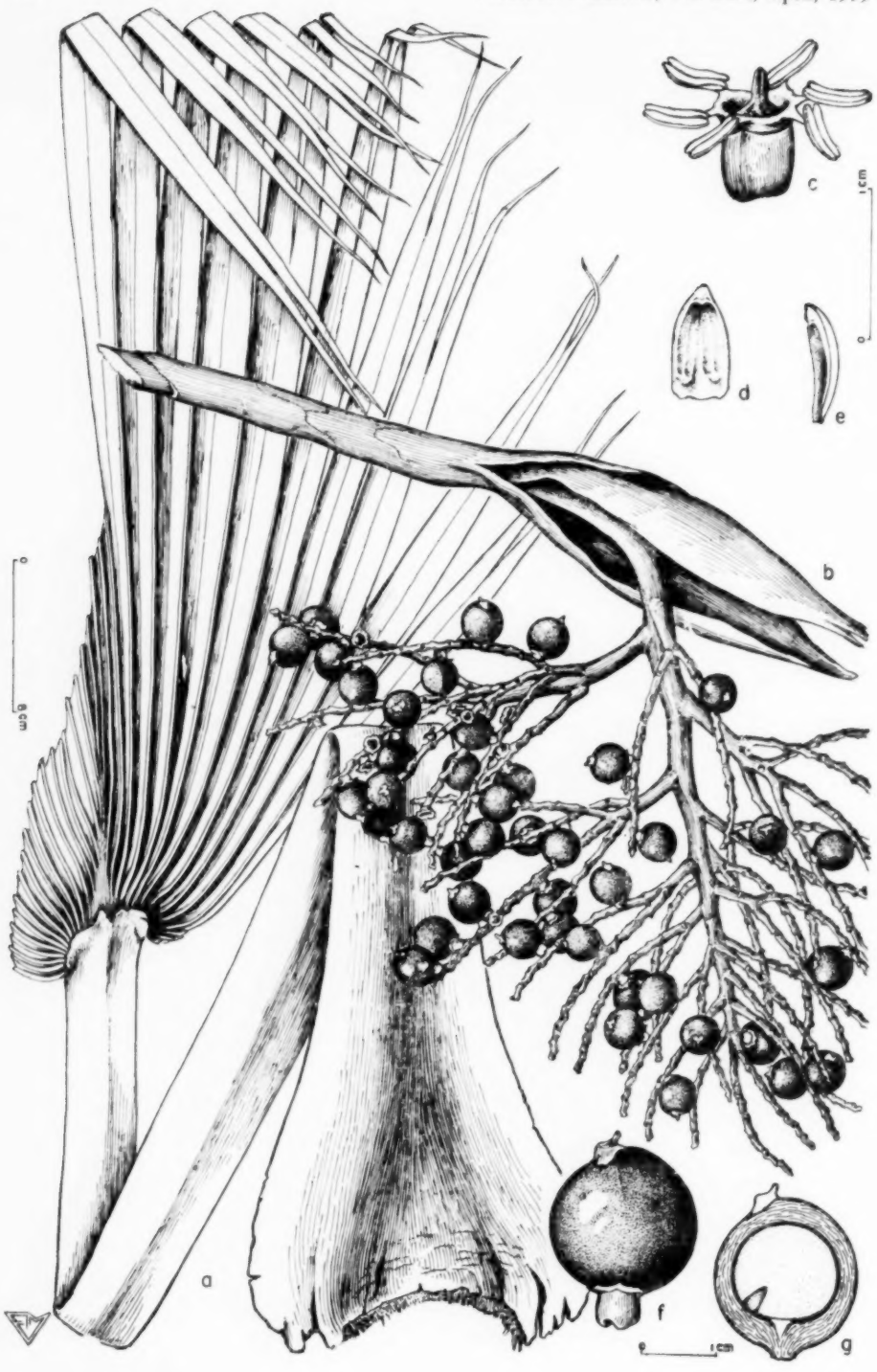
Pritchardia Aylmer-Robinsonii sp. nov.

Fig. 3

NOM. VERN.: "wahane," or occasionally "hawane."

DIAGNOSIS HOLOTYPI: Arbor, stirpe unica erecta 7 m. alta, 2 dm. diametro, summa turbinata densa 35–40-folifera, foliis adscendenti-divergentibus, deinde foliis marcidis pendentibus, petiolis 92 cm. longis in basi 19 cm. latis in apice 3.7 cm. latis clariter viridibus glabris, scutello 2–4 cm. longo glabro valde obliquo late obtuso apice anguste acuminato fugaceo, laminis 1 m. longis clariter viridibus et in maturis in lateribus ambis glabris, segmentis multis per 4 dm. partitis apicibus bilobatis tenuibus pendulis sensim diminuentibus acutisque, paginis ambis cum nervulis transversis minute striatis, segmentis centralibus in basi 17 mm. latis, segmentis immaturis complicatis infra in costis et petiolis dense fusco-lanatis, pilis omnibus similibus gracilibus et implicatis vel cum lepidiis paucis permixtis, spadicis glabris apicibus liberis expansis 15–20 cm. longis anguste ellipticis concavis, inflorescentiis geminatis 6–9 dm. longis glabris, pedunculis 40–55 cm. longis, paniculis 25–30 cm. longis, 25–30 cm. diametro ovoideis, ramis secundariis ferentibus 2–9 ramulis floriferis 4–13 cm. longis 2–4 mm. diametro glabris, bracteis et alabastris in exemplare desunt, calycibus 4 mm. longis minime tridentatis subcylindricis, nervis obscuris sed in apicibus ad dentibus manifestis et convergentibus, petalis 7.5 mm. longis 3.8–4 mm. latis ellipticis in basi truncatis intra cum impressio antherarum sulcatis caducis, circulo staminali extra calycem 1–1.5 mm. exserto et distento, filamentis rotatis parte libera 1.5–2 mm. longa, antheris 4.5 mm. longis divergentibus anguste oblongis obtusis et emarginatis, ovario sulcato apici conico, stigmati trigonali truncato, fructibus orbicularibus 18–20 mm. diametro nigris duris, pericarpiis 2.5–3.5 mm. crassis, mesocarpiis grumosis et fibrosis pallidis, endocarpiis 0.5 mm. crassis brunneis, testis levigatis atrobrunneis, endospermiis albis osseosis, perianthiis fructiferis 3.5–4 mm. longis 4–5 mm. latis subcylindraceis a latere compressis.

Tree with single erect trunk 7 m. tall, 2 dm. in diameter; crown turbinate, dense with the numerous (35–40) leaves, ascending, spreading, then on withering becoming pendent, and the inflorescences making the same descending, semicircular course of movement; petiole 92 cm. long, 19 cm. wide just above the base, 3.7 cm. wide at apex, after expansion bright green, glabrous; scutellum 2–4 cm. long, glabrous, very oblique, broadly obtuse with a narrow acuminate, fugaceous apex; blade parted into numerous segments, measuring 1 m. from the ligula to the apex, bright green and glabrous on both sides long before maturity; segments parted for about 4 dm., rather thin and drooping, deeply parted into two, gradually tapering acute tips; both surfaces finely striate with oblique transverse veinlets; central and largest segments 17 mm. wide at their disjunction points; young unexpanded leaves having the back of the petiole and the costae of the lower blade surface densely lanate with a fawn-colored coat, the hairs fine and tangled, uniform or mixed with a few lepidia; spadices glabrous, the free expanded tips 15–20 cm. long, narrowly elliptic, concave; inflorescences paired, 6–9 dm. long, glabrous; peduncle 40–55 cm. long; panicle 25–30 cm. long, 25–30 cm. in diameter, ovoid; secondary branches bearing 2–9 floriferous branches, these 4–13 cm. long, 2–4 mm. in diameter, slightly zigzag between the nodes, glabrous; bracts and buds not collected; calyx 4 mm. long, perceptibly 3-toothed, subcylindric, nerves obscure but their tips visible and converging towards the calyx teeth; petals 7.5 mm. long, 3.8–4 mm. wide, elliptic, the base truncate, the apex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subacute, thick and coriaceous, within longitudinally furrowed by the impress of the anther sacs, caducous; staminal ring exserted 1–1.5 mm. beyond the calyx and wide flaring; filaments diverging almost horizontally, the free part 1.5–2 mm. long; anthers 4.5 mm. long, divergent, narrowly oblong, obtuse and emarginate; ovary with the exposed tip conical, furrowed and ridged below; stigma trigonous, truncate; fruit spherical, 18–20 mm. in diameter, black, hard; pericarp 2.5–3.5 mm. thick; mesocarp grumous and fibrous, pale, endocarp 0.5 mm. thick, brown; seed coat smooth, dark brown; endosperm white, bony; fruiting perianth subcylindric, 3.5–4 mm. long, 4–5 mm. wide, laterally compressed.

HOLOTYPUS: Niihau, Mokouia Valley, south ridge of, knoll, protected by basalt boulders, 875 ft. alt., August 15, 1947, *H. St. John 22,813* (BISH).

This new species of palm was the most interesting find made during the visit to Niihau, and is a vivid reminder of the various other indigenous plants that doubtless formed a scrub or forest growth on the uplands, before their destruction by grazing animals. First a single palm tree was seen, at the head of the entrenched lower part of Haao Valley at 250 feet altitude. It was rooted in a rugged rocky talus just below the cliffs forming the cirque-like head wall. The trunk was about 15 meters tall and 30 centimeters in diameter, and it projected high above the cliff walls. The crown was unhealthy, and there were no inflorescences, probably due to a large hole bored into the trunk near the apex, probably by some animal. The next specimens were seen on the south divide of Mokouia Valley at 875 feet altitude, on the top of a prominent summit. Here in a forbidding jumble of great basalt boulders was one tree, healthy, and in flower and fruit, and it furnished the type specimens. At its foot were several seedlings with good leaves, but scarcely any trunk developed as yet. The crown of the large tree was dense and it bore many inflorescences in flower and fruit. The writer shinnied up the trunk, 7 meters tall, grasped a lower leaf and hung there to rest, but then was too tired to scramble into the crown. He cut off a leaf, inflorescences with flowers and ones with fruits, then slid exhausted down the trunk. More specimens could have been obtained by felling the tree, but to do that to a rare survival near extinction would have been vandalism. A third grove was shown to the collector on the lower north slope of Kapaka Valley which is the next major valley northeast of Mokouia Valley, and debouching on the plain about one eighth mile east of Puu Alala. Here, rising out of a tangle of *Prosopis chilensis* trees, was a small clump of the *Pritchardia*, several smaller ones and two mature trees reaching about 7 and 10 meters in height. The native guide who knew the island thoroughly did not know of any other existing trees. These few survivors were in localities where the rugged and steep rocky slopes gave them some protection from the grazing sheep and cattle. Even so, the species is on the point of extinction.

The new species is named in compliment to Aylmer F. Robinson, in recognition of his keen interest in and wide knowledge of the natural productions of Niihau. His suggestions made the time in the field much more productive, and he has kindly reviewed both the botany and the Hawaiian names in this report. It is a pleasure to name this Niihau tree for Mr. Robinson.

The report by David Samuel who visited Niihau on January 29, 1778, with Captain Cook, that he saw "two or three palm trees," might have referred to the new species of *Pritchardia*, or to *Cocos nucifera*. From the vague nature of his statement, it is not now certain what palm he saw. His words are quoted by Handy (1940: 153).

FIG. 3. *Pritchardia Aylmer-Robinsonii*, from the holotype: *a*, leaf × ¼; *b*, fructescence × ¼; *c*, flower × 2; *d* and *e*, petals × 2; *f*, fruit × 1; *g*, fruit in longitudinal section × 1.

AMARANTHACEAE

Nototrichium sandwicense (Gray ex Mann) Hbd. var. ***niihauense*** var. nov.

Fig. 4

DIAGNOSIS HOLOTYPI: Frutex 1–3 m. alta, laminis 5.7–15.8 cm. longis, 2.8–9.1 cm. latis, spicis 2–6 cm. longis recurvatis pervillosis et floribus clausis, bracteis rhachidis 2–2.5 mm. longis, bracteis florarum 2.3–2.7 mm. longis, sepalis 3–3.5 mm. longis obscure plurinervosis dense albo villosis in omnibus partibus excepta margine, antheris 0.5 mm. longis cellulis connectis.

DESCRIPTION OF ALL SPECIMENS: Shrub 1–3 m. tall, as much as 2 cm. in diameter at base; petioles 8–25 mm. long; blades 5.7–15.8 cm. long, 28–91 mm. wide, ovate, obtuse, abruptly cuneate and short decurrent, above short appressed pilosulous, below whitened by the appressed pilose tomentum; peduncles 3–30 mm. long, 2-bracted; spikes 2–6 cm. long, 8–10 mm. in diameter, recurving and the tips pendent, the axis pilose, with glabrous, scarious lanceolate bracts 2–2.5 mm. long, these exposed after the shedding of the fruits; flowers almost hidden by the abundant silky villosity, the paired bracts persisting below the flower 2.3–2.7 mm. long, sparsely pilose or villous; the four sepals 3–3.5 mm. long, broadly lanceolate, densely white villous except near the margins; stamens 3/5 the length of the perianth; filament ring prominent, dark; anthers 0.5 mm. long, oblong-ellipsoid, the cells joined; ovary subglobose; utricle 1.5 mm. long, cylindric, transparent; seed 0.5 mm. long, brown, obliquely elliptic.

HOLOTYPUS: Niihau, first valley west of Kaali Cliff, top of steep basalt talus, 100 ft. alt., shrubs 1–2 m. tall, August 16, 1947, *H. St. John 22,830* (BISH).

SPECIMENS EXAMINED: Niihau, Mokouia Valley, basalt rock beneath *Prosopis* tree, 700 ft. alt., March 30, 1949, *H. St. John 23,589*. It was also observed by the writer, but not collected, on Kaali Cliff.

The holotypic collection is abundant and with abundant flowering and fruiting spikes, but not a whole leaf was left on the plant. Some insects had eaten of the foliage, till the leaves were reduced to a mere lacework. The second collection, made after a heavy winter rain, has lush new growth and unharmed leaves. A branch of this is shown on the illustration (Fig. 4) and may be classed as a paratype.

No Hawaiian vernacular name for this species was known to the informant, Kalani Niau. Being a large and conspicuous shrub, a specimen was taken to the village and shown to the best informed, older native Hawaiians, but none knew a name for it. This is regretted, for as a perusal will show, the natives of Niihau still remember the Hawaiian vernacular names for almost all of the native plant species, and they have given Hawaiian names to most of the well-established adventive and cultivated species.

These are the first available collections of *Nototrichium* from the island of Niihau, so it is not surprising to have them turn out to be undescribed. There is an earlier record by Forbes (1913: 21) of this species from Niihau in his account of the Stokes collections. This early collection is lost. It is not now to be found in the Bishop Museum, and it does not appear in their card index of the herbarium as ever having been inserted in the collection.

The closest relative seems to be var. *longespicatum* Hbd. from Molokai (and perhaps formerly from Maui). This differs by having smaller blades, the principal ones 4–6 cm. long and 2.5–4.2 cm. wide; shorter spikes 2.5–5 cm. long, usually straight, less hairy, and with the flowers well exposed; bracts of the rhachis 1.5–2 mm. long; floral bracts 1.5–2 mm. long; sepals 2.7–3.2 mm. long, strongly 5–9-nerved, villous at base, the hairs diminish and becoming few on the pilose back, the apex and broad margins glabrous; anthers 0.2 mm. long, the cells separate, much diverging towards the base. On the other hand var. *niihauense* has the

Fig. 4. *Nototrichium sandwicense* var. *niihauense: a*, habit × 1; *b*, inflorescence × 1; *c*, flower × 8; *d*, utricle × 8; *e*, funiculus and seed × 8; figs. *b*, *c*, *d*, *e* from holotype; fig. *a* from St. John 23,589.

blades 5.7–15.8 cm. long, 2.8–9.1 cm. wide; spikes 2–6 cm. long, recurving and with pendent tips, and so villous that the flowers are almost concealed; bracts of the rhachis 2–2.5 mm. long; floral bracts 2.3–2.7 mm. long; sepals 3–3.5 mm. long, obscurely several nerved, densely white villous except near the margin; anthers 0.5 mm. long, the cells joined.

In Mann's Enumeration (1867: 200) was also published *Ptilotus Sandwicensis* Gray ex Mann, var. *β Kavaiensis* Gray ex Mann. Sherff has recently (1951: 16), following Hillebrand (1888: 373), taken up this as *Nototrichium sandwicense* var. *kauaiense*. In Hillebrand's time the rules of nomenclature were less precise and, as was customary, authors assumed the right to "correct" the spelling of names of taxa, particularly those derived from geographic place names. Hillebrand changed all previously published names like: *maviensis*, *kavaiensis*, *owhyhensis*, and *wahuensis* to *maniensis*, *kauaiensis*, *hawaiiensis*, and *oahuensis*. The recent international codes of nomenclature (Amsterdam 1935, Stockholm 1950, and Paris 1954) do not permit this free alteration of validly published scientific names (1954 code: art. 73). Unless it can be proved that the original author made a typographical error or a mistake in spelling, his scientific name must be retained as published. Once-current geographic names are not now erroneous, even though a different spelling of the geographic name has been officially adopted and standardized. In latinizing the Hawaiian name Kauai, Gray chose to render the letter u by the Latin v, and he had good precedent for this course. Hence, even though Sherff in his revision of the genus has adopted the spelling *kauaiensis*, one must in conformity with the rules return to the original spelling: *Nototrichium sandwicense* var. *kavaiense*. It is given a neuter ending, because the varietal name must agree in gender with that of the genus, in this case it being neuter.

Since it has not been illustrated, there is included here a drawing made from the holotype: Kauai, Hanapepe, Mann & Brigham 590 (GH), of *N. viride* Hbd. var. *viride* (Fig. 5).

LEGUMINOSAE

Abrus precatorius (L.) L. forma *luteoseminalis* forma nov.

Seminibus pallide luteis. Seeds pale yellow.

NOM. VERN.: "pukeawe lenalena" (=Yellow Pukeawe). On the larger Hawaiian Islands the vernacular name "pukeawe" is applied to the native shrubs in the genus *Styphelia*.

HOLOTYPUS: Niihau, Nonopapa, 20 ft. alt., in scrub on dry limestone flat, seeds pale yellow, August 13, 1947, *H. St. John 22,768* (BISH).

The typical form of the species with black-ended scarlet seeds occurred near by, but in one section of the thicket all the plants produced wholly seeds that were of a pale yellow color. This is not a common form of the species, and seems to have been mentioned previously only by Pollacci (1918: pl. 18, fig. 10). The new name is from the Latin *luteus*, yellow, *seminalis*, pertaining to a seed, in allusion to the seed color.

Erythrina sandwicensis Degener var. **sandwicensis** forma **sandwicensis**

E. sandwicensis Degener, Fl. Haw. fam. 169c: 12/5/'32, with fig.

E. monosperma Gaud., Voy. Freyc. Uranie, Bot. 486, 93, (1826) [=1830]; and Atlas pl. 114, 1826–30; not *E. monosperma* Lam. (1786)=*Butea monosperma* (Lam.) Taubert.

Corollas orange, or varying from yellow to scarlet; seeds bright red.

The name *E. sandwicensis* Degener was merely a renaming of the long known common lowland tree first called *E. monosperma* Gaud., this name having proven invalid, being a later homonym. Hillebrand, Rock, and other Hawaiian authors had accepted this tree as indigenous in both Hawaii and Tahiti, and listed as a synonym *E. tahitensis* Nad., described from a locality at 700–800 meters

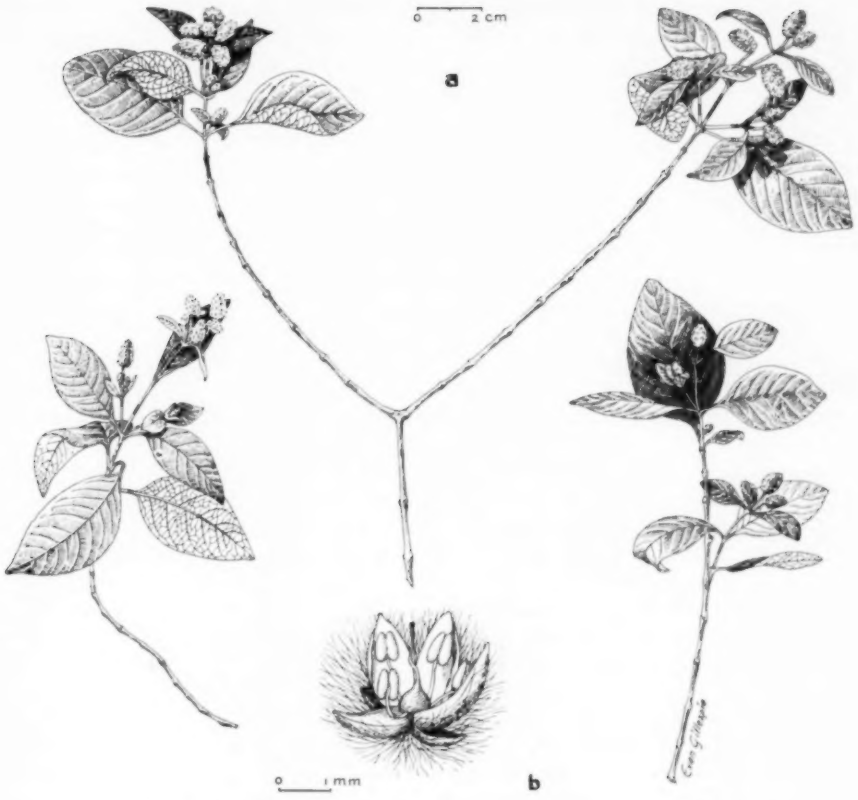

Fig. 5. *Nototrichium viride* var. *viride*, from isotype: *a*, habit × ½; *b*, flower × 8.

in the mountains of Tahiti. Degener gives the new name *E. sandwicensis*, and his publication is valid, though it is not well documented. He says merely, not *E. tahitensis*, giving no differentiating characters to separate his newly named species from the Tahitian one. Later, Krukoff (1939: 226–227) discussed the relationship between *E. sandwicensis* Degener and *E. tahitensis* Nad. "The rediscovery of the very rare *E. tahitensis* in Tahiti seems to be essential for ascertaining the nomenclatural status of the Hawaiian plant now known as *E. sandwicensis*. I have seen *Nadeaud 499* (type of *E. tahitensis*), deposited at Geneva. It consists of a single inflorescence with small flower buds, two flowers, one pod, one seed, and no leaflets. From this available material it is impossible to decide whether or not the plant is specifically distinct from the plant native to Hawaii."

The writer had studied the original description of *E. tahitensis* Nad. It is detailed and 12 lines long. The following characters seem diagnostic. They are, in translation: lateral leaflets cordate, acuminate, glabrous; calyx 4-toothed; keel broad, rounded, emarginate; stamens monadelphous; seeds orange. After the writer studied the collections of *Erythrina* in Paris and Geneva, he was able to complete the description of *E. tahitensis* Nad. and to

establish it as distinct from the Hawaiian *E. sandwicensis* Degener (see St. John, 1955: 293–299).

Degener gives under his new name, *E. sandwicensis*, a list of synonyms and usages, but the earliest and the basic one is *E. monosperma* Gaud., the first name given to the Hawaiian "wiliwili" tree. This is confirmed by the fact that Degener gives a type locality: "In insulis Sandwicensibus (Alt. 350–400 hex.)." This is a quotation from the single locality given by Gaudichaud for his new *E. monosperma*. Hence, Degener's concept rests primarily on that of Gaudichaud. Gaudichaud obtained a specimen and this was illustrated in his atlas in detail, showing stem, leaves, buds, flowers, fruit, seeds, and details. He mentions the plant in his phytogeographic discussion (1827: 93) where he describes the second region, where, after leaving the lowland cultivated areas, and entered as one begins to ascend and to encounter the first indigenous plants, but he gives no further details here, other than the vernacular name, "ouiliwiri." His brief description (1830: 486) is here quoted:

"1. Erythrina monosperma. Pl. 114.

E. arborea; inermis; foliolis late ovato-reniformibus, obtusis, subtus calycibusque molliter fuscenti-tomentosis; fructibus monospermis.

In insulis Sandwicensibus (Alt. 350–400 hex.)."

There are trees or branches of trees of the "wiliwili" that are unarmed, but usually there are numerous branches beset with short spines, so the unarmed branches are not diagnostic. The smaller pods may be 1-seeded, but much more characteristically the pods are several-seeded. Gaudichaud's description omits mention of the color of flower or fruit, but in the Explanation of Plates in his Atlas (1826–30: 21) for plate 114, fig. 9, he states, "Graine rouge foncé. . . ." Thus we know that his specimen was red-seeded, but the color of flower was not recorded. The flowers are fleshy, and are borne in heavy, dense racemes, so that even today, with the best drying methods using artificial heat, it is expected to have the flowers fade to dull brown.

Degener (1932: family 169c) describes his *E. sandwicensis*, as with, "Standard . . . orange-red to rarely yellow or even white . . .; wings greenish yellow . . .; keel greenish yellow. . . ." This seems a composite description of the plant population that he included in the species, but it is clear that he included the common form of the species which has the corollas orange or shading from yellow to scarlet. In some, the bases of the corollas are greenish, but the predominant colors are as stated above. This color form is also the biological type of the species, and the writer here chooses it as the nomenclatural type. In the Bishop Museum the specimens of this forma *sandwicensis* for which there is record of the color, have it given as follows: orange, orange, orange, red, green and pink. Various other botanists in Hawaii have published accounts of the tree now called *E. sandwicensis*, and below are quoted their descriptions of the flower colors. Mann wrote (1867: 185) flowers "red, much the color of red coral, with some yellow, showy." Mrs. Sinclair said (1885: pl. 18 with text), "The flowers vary in colour from pale yellow to orange scarlet. There is no perceptible difference in the trees, but the natives say the wood of those with scarlet flowers is slightly harder and more durable than the other. . . ." Her colored plate shows the corolla orange blending to scarlet, the seeds bright red. Hillebrand (1888: 99) stated, flowers "pale red or orange, rarely yellow." Rock recorded (1913: 191) the "flowers pale yellow or brick red. . . ." Then later (1919: 49), flowers "brick red, orange or pale yellow." He later repeats this same description (1920: 183). Degener's flower description has already been quoted. Nearly all of these writers agree that the tree has flowers that are orange or yellow shading to scarlet. This is the kind here selected as the type form. The other ones with different flower colors are here described as color

forms, and one new seed color is distinguished. C. Judd (1920: 96) stated that the "blossoms vary in color from an orange scarlet to pale yellow." There is an early collection from Niihau, Foot of Plateau, S. E., January 1912, *J. F. G. Stokes*. This now has faded, brown flowers, and is without color notes. However, the native informants on Niihau reported that the majority of the trees had orange flowers and red seeds.

One of these color forms was marked in the herbarium by Dr. Rock with a name as a new variety. We refrain from adopting this name of his, since in his three publications on the subject he did not publish it, and apparently has not done so elsewhere. It seems that he decided not to publish it. In any case, the writer treats the plant not as a variety but as a forma.

E. sandwicensis Degener forma ***alba***, forma nov.

Floribus albis. Corollas white.

HOLOTYPUS: Oahu, between Koko Crater and Makapuu, level plain, alt. 30 m., tree 6 m. tall, flowers white, April 19, 1931, *E. P. Hume 187* (BISH).

E. sandwicensis Degener forma ***lutea***, forma nov.

Floribus luteis vel luteo-viridibus. Corollas yellow, greenish yellow, or yellowish green; seeds red.

HOLOTYPUS: Niihau, Apana Valley, 400 ft. alt., rocky dry gulch, tree 6 m. × 2 dm., flowers yellowish green, seeds red, August 14, 1947, *H. St. John 22,806* (BISH). Vernacular name: "wiliwili."

SPECIMENS EXAMINED: Molokai, Kamalo, Kapulei Ridge, arid rocky region, common, June 25, 1928, *O. Degener 7,216*.

Maui, East Maui, Ulupalakua district, fl. greenish yellow, August 26, 1948, *Karl H. Korte*.

Lanai, Mauna Lei, July 13, 1910, *J. F. Rock 8,118;* Paomai, yellow flowered, September 14, 1913, *G. C. Munro 39*, and *94*, these last two probably being duplicates.

All but one of these collections are leafless, as this is the common condition at anthesis.

E. sandwicensis Degener var. ***luteosperma***, var. nov.

Seminibus luteis, corollis pallide viridibus. Seeds dull yellow; corollas pale green.

HOLOTYPUS: Niihau, Nonopapa, 20 ft. alt., thicket on dry flat, tree 7 m. × 2 dm., fl. pale green, seeds dull yellow, August 13, 1947, *H. St. John 22,769* (BISH). Vernacular name: "wiliwili lenalena."

No other collections of this are known. Since it has distinctive color characters of both flower and seed, it is classed as a variety.

ARALIACEAE

Cheirodendron trigynum (Gaud.) Heller var. **Hillebrandii** Sherff

Panax ovatum H. & A., Bot. Beechey Voy. 84, 1832. (See Fig. 6.)

Not found by any recent collector, its record being from a collection by Lay and Collie of the Beechey Voyage (Hooker and Arnott, 1832: 84). It is certainly extinct now. This collection, the holotype of *P. ovatum*, is in the herbarium at Kew. A complete revision of the genus *Cheirodendron* in Hawaii has just been published by Sherff. In this he mentions (1954: 3, 4) *Panax? ovatum* H. & A. and discusses (1954: 28) its placement. He repeats the descriptive characters given by Hooker and Arnott, but does not definitely place the species or key it. He tentatively suggests (1954: 27) that it is a synonym of *C. trigynum* (Gaud.) Heller var. *halawanum* Sherff. Because the holotype of *P. ovatum* was a sterile specimen, one cannot be positive as to its identity. However, Sherff's placement of it in var. *halawanum* does not seem to be justified. This variety, known from abundant collections on Oahu, Molokai, and Lanai, has the petioles 4–10 cm. long; the lateral petiolules 7–34 mm. long; the terminal petiolules 17–42

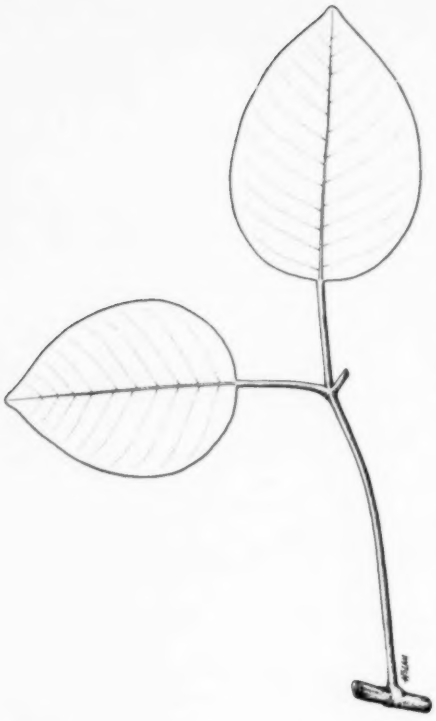

FIG. 6. *Panax? ovatum*, from holotype: *a*, leaf × ½.

mm. long; the leaflets when dried, thinnish, obsoletely to sharply 1–9-denticulate, and the lateral ones 28–63 mm. wide, and the terminal ones 44–75 mm. wide. *P. ovatum* H. & A. has, on the other hand, the petioles 7.5–11 cm. long; the lateral petiolules 22–30 mm. long; the terminal petiolules 26–38 mm. long; the leaflets when dried, thick chartaceous to subcoriaceous, entire, the lateral ones 50–60 mm. wide; and the terminal ones 55–65 mm. wide. This is the third species that was described in the group that is now called *Cheirodendron*. The type specimen is well preserved and is available in the Kew herbarium. The writer studied it there in 1954. The accompanying drawing shows a leaf from this holotype. It is not clear why Sherff did not examine it, as it is available at Kew, and he studied and cited other specimens from the Kew herbarium.

It is possible that *P. ovatum* H. & A. is a species endemic to the island of Niihau, but there seems no chance of establishing that now, as the native forest has vanished and this species has not been found there by any of the recent collectors. The island of Kauai is nearest to Niihau, being only 9 miles distant. There are, according to Sherff, four species and six varieties of *Cheirodendron* on Kauai. None of them has foliage matching that of the Niihau tree. The next closest island, Oahu, is about 120 miles away. Though all described taxa have been checked, it seems that it is most like a variety that occurs on both mountain ranges of Oahu, *C. trigynum* var. *Hillebrandii* Sherff. This variety usually has the leaflets serrate and elliptic or elliptic-lanceolate to elliptic-ovate. However, there are some collections of it with entire and broader leaflets, ovate, entire, abruptly obtuse, and with long petiolules. These exactly match the holotype of *P.? ovatum* H. & A. When and if fertile material of the Niihau plant is found, the taxonomic placement can be reviewed. Till then the best placement seems to be as a synonym of *C. trigynum* (Gaud.) Heller var. *Hillebrandii* Sherff.

Reynoldsia sandwicensis Gray

NOM. VERN.: "'ohe'ohe."

The only record of this is in the publication by C. N. Forbes (1913: 23) on the collection by J. F. G. Stokes. The species is listed without comment. The specimen is not now in the Bishop Museum nor does it appear in the card catalogue of the herbarium as ever having been inserted there. When exploring Niihau in 1947 the writer did not see the tree. It was one of the four native trees reported by Forbes, so its rediscovery was much desired. When asked, the guide K. Niau immediately replied that he knew the "'ohe'ohe," that it was now very rare. He said there was only one living tree left, and he then led the way on August 13th to a spot on a steep side

of upper Kanaha Valley. At the site which he knew, there was now no sign of a tree, it having died and the soft stems having rotted away since the guide's last visit to the spot. Without doubt it is now extinct on Niihau. The record is a credible one, as the tree once, and to some degree still, makes a scattered arborescent growth on the low, very dry sections of all of the Hawaiian Islands. In the revision of the genus by Sherff (1952: 7), he states, "I have seen as yet no specimens from Kauai, Niihau, or Kahoolawe."

SOLANACEAE

Solanum Nelsoni Dunal var. Nelsoni

S. Nelsoni Dunal in DC., Prodr. 13: 123, 1852.
S. laysanense Bitter, Nat. Ver. Bremen, Abh. 16(3): 432–435, pl. 4, fig. A–D, 1900.
S. nelsoni Dunal var. *typicum* F. Br., in Christopersen & Caum, Bernice P. Bishop Mus., Bul. 81: 35, 1931.
S. nelsoni Dunal var. *intermedium* F. Br., l. c. 35–36.
S. nelsoni Dunal var. *caumii* F. Br., l. c. 36.
S. nelsoni Dunal var. *acuminatum* F. Br., l. c. 36.

NOM. VERN.: "akia."

Niihau, south end, sand country; also cliff at, November 1, 1939, *G. C. Munro;* Kawaewae, under *Prosopis* thicket, 75 ft. alt., *St. John 22,731;* Leahi, in coral sand near beach, 10 ft. alt., *St. John 23,621.*

Two isotypes of *S. laysanense* as well as the holotypes and the paratypes of the varieties of *S. Nelsoni* described by Dr. F. B. H. Brown and all the specimens in the Bishop Museum have been studied. The shrubs are all similar; the flowers are identical; the fruits essentially so, though the collectors recorded a few as with red berries, while the majority recorded black berries. The berries recorded as red when fresh are now black when dried. There is some apparent variation in the size of the berries, but as they were juicy, then were pressed, the variation does not seem significant. The seeds are identical. The leaves vary in shape from cordate to orbicular, ovate, or elliptic; the base from cordate to rounded, truncate, or cuneate; the apex from obtuse to acute; the margin from entire to slightly or markedly sinuate. The measurements of the hairs meet or overlap, and the leaf shapes are variable and difficult to define. Upon these characters the species and varieties listed have been described. The larger the leaves, the more apt they are to be acute at apex and with sinuate margins. An isotypic sheet of *S. laysanense* shows some blades subcordate at base, as well as ones rounded or cuneate. The holotype of *S. Nelsoni* var. *acuminatum*, Caum 68 from Nihoa I., has most of the blades sinuate, a key character, but several adult leaves on the same branch are entire. The same is true on an isotype, while on a second isotypic sheet, most of the blades are entire, while only a few show a slight waviness in the margin. The holotypes and isotypes of var. *Caumii* and var. *intermedium* are relatively constant to the characters alleged. *S. Nelsoni*, as shown by a photo of the holotype, David Nelson, from the Sandwich Islands, and by the several recent collections from Molokai, is relatively constant in its cordate, entire blades, but one sheet of several collected by Rock, March 1910, from Momomi (=Moomomi) beach, Molokai, shows both leaves with cordate bases and ones with rounded bases on the same stem. *S. Nelsoni* var. *intermedium* was keyed as having the leaves cordate to subacute at the base, and the several specimens show stems with leaves that are cordate, rounded, or subcuneate at base.

At hand are two unmounted collections with numerous duplicates. These would be classified as *S. Nelsoni* or its var. *typica*. *St. John 19,962* from Moomomi, Molokai, consists of 22 separate plants or branches. Mostly these show small, cordate, entire blades, but four bear also some leaves that are shallowly sinuate. *St. John 22,731* from Kawaewae, Niihau, consists of numerous sheets with a total of 50 branches. These all have the leaves cordate or ovate-cordate, obtuse or subacute, and

most of them entire. Four of them have some of the blades slightly sinuate, and one has a single large leaf strongly sinuate. From this review of the characters of the leaves, the writer is convinced that the shapes and shallow lobing of the leaves mentioned are mere fluctuations in a single population and usually on the same individual branch. Hence, the specific and varietal names based upon plants showing these characters are here reduced to the synonymy of *S. Nelsoni* Dunal.

Early there was described another variety, *S. Nelsoni* var. *thomasiaefolium* Seem. (Jour. Bot., Brit. and Foreign 1: 209, 1863), based upon a collection by T. Nuttall on Atoi (=Kauai). This may well be the greatest extreme among the lobed-leaved plants. At hand is a photo of the type in the British Museum. Three years after publishing the variety Seeman again listed it (1866: 174) and repeated this original account; "foliis cordato-ovatis sinuato-lobatis, lobis (5–7) obtusis vel cordatis integris. . . . This has quite the look of *Thomasia solanacea*, Gay, and would probably be described as a new species by anyone not having seen the evident transition there is in some specimens of what Nuttall has called *S. rotundifolium* and A. Gray justly considers identical with the original *S. Nelsoni*, Dun., preserved at the British Museum. In these specimens some of the leaves have a tendency to become sinuato-lobate, whilst again several leaves of my var. *thomasiaefolium* are cordate and entire." The photo of the holotype confirms this, that there are several leaves that are cordate and entire, but mostly they are strongly sinuately lobed, with two large, sinuate lobes on a side, cut half-way to the midrib. Seeman well states the inconstancy in this group of the characters of leaf shape and lobing, and the writer has stated his observations on the same points. However, no recent collections or any others seen show blades with the deep rounded lobes like those of var. *thomasiaefolium*. It is a marked extreme, and no intermediates have been seen that fill in the gap. Hence, until the variety is again collected and more knowledge can be gained of its variability and occurrence, it seems best to accept var. *thomasiaefolium* as a variety, peculiar to Kauai. The writer and his several assistants searched for it in December, 1947, on the sandy shores of Kauai without success.

The treatment of this group by Dr. F. B. H. Brown (1931: 37) raises a question of typification. He gives a generalized description for *S. Nelsoni* Dunal (as *nelsoni*), then a detailed one for each of the four varieties, including var. *typicum* F. Br., new var. As var. *typicum* he recognized the plants with cordate, entire leaves. For this he cites only two collections, both in the Bishop Museum, and both from Moomomi, Molokai: *J. F. Rock*, March 1910, sheet A (which lettering was added to Rock's label in a later hand, apparently Brown's); and *C. N. Forbes* no. *613.Mo.* No type was designated in the publication, but in the Bishop Museum the specimens are marked: the *Rock* sheet A is marked in Brown's writing, "Type of Descript."; the *Forbes 613.Mo.* is marked in Brown's writing, "Type! of amplif. descript."; and there is a third, unlisted, sheet, *Forbes 604.Mo.*, marked in Brown's writing, "Type of amplif. descript." On checking Forbes's field number book, it is evident that both of his numbers written by him on his labels were wrong, that his collection of this *Solanum* from the sand dunes at Moomomi was no. *607.Mo.*, and that both of his sheets should be corrected to so read, as does an unmounted duplicate. Thus Brown, in describing *S. Nelsoni* Dunal var. *typica* F. Br., published no choice of a type in the bulletin, which was issued by Christophersen and Caum, but in the herbarium he marked as type three sheets collected in 1910 and 1915 by two different collectors. Not every possible detail concerning the selection of types is covered in the International Code of Botanical Nomenclature, but the practice is established and legalized. It is clearly improper to choose either the Forbes or the Rock collections to be the type of var. *typica* (now called var. *Nelsoni*). The type must be the same specimen

described as *S. Nelsoni* Dunal, that is the specimen in the British Museum collected "in insulis Sandwich," by David Nelson in 1788. There is a photo of this in the Bishop Museum. It has small, cordate, entire leaves, like the ones described by Brown for var. *typica*.

CUCURBITACEAE

Sicyos niihauensis, sp. nov.

Fig. 7

NOM. VERN.: "pua o Kama" (=the flower of Chief Kama; or perhaps merely a modification of "kaukama" =cucumber).

DIAGNOSIS HOLOTYPI: Liana annua herbacea, caulibus ad 10 m. longis supra arbores fruticesque scandentibus vel decumbentibus gracilibus pallide viridibus deinde glabratis, novellis puberulentis pilis in initio glandulosis, pilis in nodis persistentioribus, internodis 6–20 cm. longis cirrhis oppositifoliosis cum pedunculo rigido 8–30 mm. longo puberulento 2- 3-partitis, partibus 7–15 cm. longis ad basim puberulis ad apicem glabris dense spiralis, foliis multis, petiolis 13–50 mm. longis scabro-puberulentis, laminis subvariabilis sed frequentissime 4.5–11.5 cm. longis 4.2–14 cm. latis suborbicularibus tenuiter 3-lobatis digitatis cum sinibus late U-formatis 3–15 mm. profundis apicibus acutis basi profunde cordata membranaceis supra pustulato-scabris pallide viridibus cum nervis pallidioris infra dense pustulato-scabris et in nervis scabro-puberulentis marginibus subintegris nervis palmatis 3-fidis, nervis lateralibus dichotomis, ramis juvenalibus fortioribus cum laminis 6.7–9.5 cm. longis 6.2–11.3 cm. latis suborbicularibus 3–5-lobatis lobis 2.5–4 cm. longis sinibus late U-formatis marginibus subintegris vel pauce dentatis et remote apiculato-denticulatis, paniculis masculis 1.5–9.5 cm. longis glanduloso-puberulentis, pedunculo 12–70 mm. longo, pedicellis 2.7 mm. longis gracilibus, alabastris 2–3 mm. diametro forte depresso-suborbicularibus pallide lutescentibus vel albis, perianthiis in flore 8–8.5 mm. diametro tubo 1.5 mm. longo subrotato, lobis 5 inaequalibus 3–3.5 mm. longis 1.8–2.2 mm. latis late lanceo-ovatis extra capitato-glanduloso-puberulentis intra minute ita, columna staminali 1.5 mm. alta, 5 antheris 1 mm. longis hippocrepiformis, inflorescentiis femineis capitatis axillaribus, pedunculis 10–15 mm. longis 9–13-floriferis capitato-glanduloso-puberulentis, corollis epigynis patelliformis vel subrotatis extra minute capitato-glanduloso-puberulentis et intra etiam minute ita, tubo 1.2 mm. diametro, lobis 1 mm. longis elliptico-ovatis, stylo 1 mm. longo glabro, lobis stigmatis 3 ligulatis recurvatis, ovario 3–5 mm. longo anguste turbinato tertia infera nuda vel sparse hirsutula, parte supera velata cum incrementis multis digitatis vel spatulatis dense hirsutis pilis in initio minute capitato-glanduloso, capitis in fructu 12–17 mm. diametro globosis dense hirsutis, fructibus 6–7 mm. longis 5–6 mm. latis 2–3.5 mm. crassis late lanceolatis infra albo-puberulentis supra velata cum incrementis adscendentibus 1.5–3 mm. longis digitatis vel spatulatis integris vel furcatis dense catenulato-glanduloso-hirsutis, seminibus solitaribus 3.9 mm. longis 3.5 mm. latis 1.9 mm. crassis lenticularibus marginibus rotundatis, testis pallide luteis vel brunneis duris lucidis, hilo 1.9–2 mm. longo elevato cartilagineo albo simili ad duam parem labias in linea formata.

Annual climbing herbaceous vine; stems climbing as much as 10 m. over trees or bushes, or decumbent, slender, pale greenish, at length glabrate; young shoots puberulent and the hairs at first glandular, the hairs persisting longer near the nodes; internodes 6–20 cm. long; tendrils oppositifolious, with a stout rigid, common stalk 8–30 mm. long, puberulent, forking into 2 or 3 tendrils 7–15 cm. long, puberulous towards the base, glabrous towards the tip, closely coiling; leaves numerous; petioles 13–50 mm. long, scabrous puberulent; blades slightly variable in form, but the commonest shape 4.5–11.5 cm. long, 4.2–14 cm. wide, suborbicular, shallowly palmately 3-lobed, the broad U-shaped sinuses

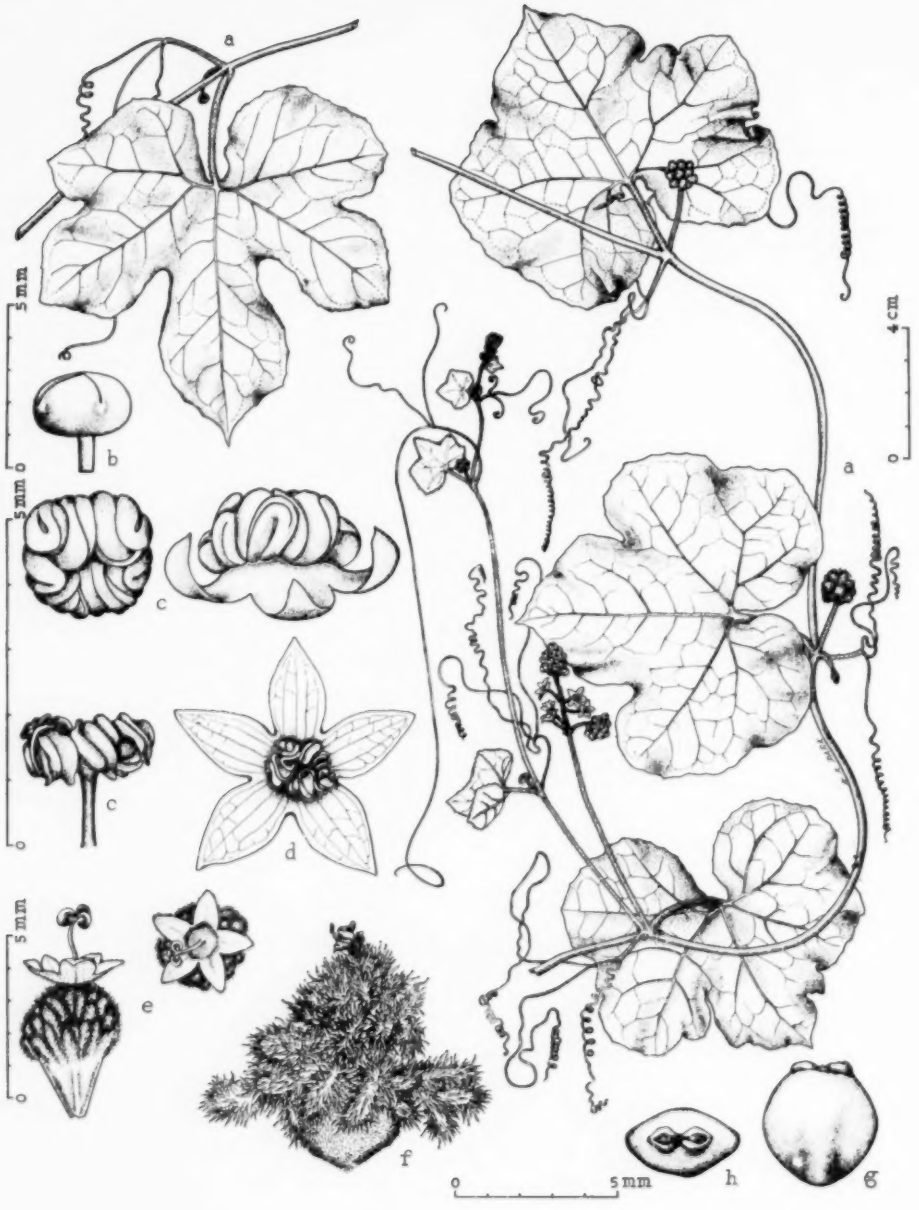

FIG. 7. *Sicyos niihauensis*, from holotype: *a*, habit × ½; *b*, staminate bud × 5; *c*, anthers × 10; *d*, staminate flower × 5; *e*, pistillate flower × 5; *f*, fruit × 5; *g*, seed, lateral view, × 5; *h*, seed, apical view, × 5.

3–15 mm. deep, the apex acute, the base deeply cordate, texture membranous, above pustulate scabrous, pale green, the veins lighter green, below densely pustulate scabrous and on the veins scabrous puberulent, the margins appearing subentire but under a lens seen with a few veins ending in minute apiculate projections, palmately 3-nerved from the base, the lateral veins forking; blades of more vigorous juvenile branches 6.7–9.5 cm. long, 6.2–11.3 cm. wide, suborbicular 3–5-lobed about halfway to base, the sinuses 2.5–4 cm. deep, wide U-shaped, the margins subentire or few-dentate and remotely apiculate denticulate; staminate panicle 1.5–9.5 cm. long, glandular puberulent; peduncle 12–70 mm. long; pedicels 2–7 mm. long, slender; bud much depressed suborbicular, 2–3 mm. in diameter, pale yellowish or whitish; perianth in anthesis rotate, 8–8.5 mm. in diameter, the tube 1.5 mm. long, almost rotate, the five lobes unequal, 3–3.5 mm. long, 1.8–2.2 mm. wide, broadly lance-ovate, capitate glandular puberulous without, minutely so within; staminal column 1.5 mm. tall; the five anthers 1 mm. long, hippocrepiform; pistillate inflorescences capitate, axillary; peduncles 10–15 mm. long, capitate glandular puberulent; pistillate flowers 9–13 in a head; corolla epigynous, shallow saucer-shaped or almost rotate, minutely capitate glandular puberulous without and even more minutely so within; the tube 1.2 mm. in diameter, the lobes 1 mm. long, elliptic ovate; style 1 mm. long, glabrous; stigma lobes 3, recurving, ligulate; ovary 3–5 mm. long, narrowly top-shaped, the lower third naked or but sparsely hirsutulous, the upper two-thirds covered with many fingerlike or thick spatulate processes and each of these densely shaggy hirsute, the hairs at first minutely capitate glandular; fruiting heads 12–17 mm. in diameter, globose, densely hairy; fruits 6–7 mm. long, 5–6 mm. wide, 2–3.5 mm. thick, broadly lanceolate, the lower part white puberulent, the upper part covered with ascending processes which are 1.5–3 mm. long, thick fingerlike or spatulate, simple or forked and densely shaggy catenulate gland-tipped hirsute; seed single, 3.9 mm. long, 3.5 mm. wide, 1.9 mm. thick, lenticular, the edges rounded, the testa pale yellow or brownish, hard, smooth, shining, the hilum 1.9–2 mm. long, raised, cartilaginous, white, shaped like two pairs of slightly open lips in a line.

HOLOTYPUS: Niihau, 1 mile W. of Kii, 50 ft. alt. (also common on Kaali cliff), grassy, sandy flats, elongate vine climbing *Prosopis* tree, leaves, pale green, veins lighter, staminate flowers white, March 29, 1949, *H. St. John 23,567* (BISH).

The closest known species is *S. pachycarpus* H. & A. of Oahu which has the petioles glabrate; blades shallowly 5-lobed; fruits 2.3–2.8 mm. wide and 1–1.8 mm. thick with the upper part glabrous; seed 2.8 mm. wide, and the hilum 0.8 mm. long. *S. niihauensis* differs by having the petioles scabrous puberulent; blades shallowly palmately 3-lobed; fruits 5–6 mm. wide, 2–3.5 mm. thick, and the upper part covered with ascending fingerlike processes, densely glandular hirsute; seeds 3.5 mm. wide, and the hilum 1.9–2 mm. long.

LOBELIACEAE

Delissea niihauensis, sp. nov.

Fig. 8

DIAGNOSIS HOLOTYPI: Frutex, caule 1–2 cm. diametro glabro, cicatricibus 9–10 mm. latis 4–5 mm. altis aggregatis stramineis depresso-scutelliformis, fasciculis 8–11 exsertis in ellipso disponitis, internodis reductis ad oras inter cicatrices congregatis, foliis glabris in fasciculo terminali denso aggregatis, petiolis plerumque divergentibus 2–4 cm. longis sed in sicco 1–1.5 mm. diametro, laminis 5.5–7.5 cm. longis 3.4–5 cm. latis chartaceis late ovatis apice acuto marginibus crenatis nervis lateralibus ad apicem diffuse ramosis, costa paulo recurvata sed lateribus foliae adscendentibus, inflorescentiis axillaribus multis tam numerosis quam petiolos obscurantur, cymis

FIG. 8. *Delissea niihauensis*, from holotype: *a*, habit × ½; *b*, flower × 2; *c*, corolla × 2; *d*, stamens and stigmas × 2; *e*, fruit × 2; *f*, seed × 20; *g*, *h*, leaves of *D. undulata*, from holotype, Paris, × ½.

17–19-pluri-floriferis divergentibus sive deflexis, pedunculis 11–16 mm. longis nudis, bracteis ad 1 mm. longis hirsutulis deinde subglabratis, pedicillis 3–8 mm. longis glabris aggregatis in cyma condensa, axile 8–15 mm. longa, hypanthiis 3–4 mm. longis ellipsoideis truncatis, dentibus calycorum 0.8–1.3 mm. longis deltoideis obtusis crassis foliaceis hirsutulis, alabastris 18–20 mm. longis subarcuatis apice in 55° decurvato, corollis in flore 22–25 mm. longis glabris subcylindricis curvatis in basi 2–2.5 mm. diametro supra majoribus in fauce 3.5–4 mm. diametro, gibbo proximo 1 mm. alto asymmetrico-conico obtuso reflexo et e basi 10 mm. distanto, gibbis lateralibus binis dimidiis et ad basem proximioribus, tubo corollae 10 mm. longo, labia supera bilobata sino 8–10 mm. longo, lobis 1.7–1.8 mm. latis ligulatis subito diminuendibus ad apicem obtusam decurvatis, labia infera subaequaliter trilobata sinibus 7–9 mm. profundis, lobis 1.5–1.7 mm. latis subiter ad apicem subacutam contractis, lobis corollae intra sparse papillosis, columna staminalis 17–21 mm. longis paene decurvatis glabris pallidis, antheris superis 8–8.5 mm. longis glabris, antheris inferis binis 6–8 mm. longis in apice penicillatis pilis hispidosis 1.5–2 mm. longis albis, stigmatibus exsertis 1–1.3 mm. convexis, ovario 1.5 mm. longo ellipsoideo, baccis 6–7 mm. diametro globoso-turbinatis apophysatis subviridescentibus, seminibus 1.4–1.5 mm. longis 0.7–0.9 mm. latis 0.2–0.3 mm. crassis ellipticis compressis cum jugis transversis sinuosis parallelis in parte muriculatis, marginibus e rhaphi prominenti crassi straminei, lateribus brunneis.

Shrub, apparently erect and single stemmed, stature unknown; stem 1–2 cm. in diameter below the lowest leaf, glabrous, the surface covered with the crowded straw-colored leaf scars 9–10 mm. wide, 4–5 mm. high, depressed shield-shaped, the 8–11 bundle scars protruding, in a broad ellipse complete except at top; internodes inconspicuous, merely pale brown protruding rims between the crowded leaf scars; leaves glabrous, numerous, in a terminal dense plume, the petioles mostly diverging; petioles 2–4 cm. long, when dried 1–1.5 mm. in diameter; blades 5.5–7.5 cm. long, 3.4–5 cm. wide, chartaceous, broadly ovate, the apex acute, the margin crenate, lateral veins 7–9 on a side, arched ascending, becoming diffusely branched near the tip, the midrib gently recurved, the sides of the leaf upturned, so that the blade will not lie flat; inflorescences axillary, numerous, forming a mass so dense as to obscure the petioles; cymes 17–19-more-flowered, divergent or deflexed; peduncle 11–16 mm. long, naked; bracts subtending the pedicels nearly 1 mm. long, at first hirsutulous, later subglabrate; pedicels 3–8 mm. long, glabrous, crowded on the condensed cyme with the axis 8–15 mm. long; hypanthium 3–4 mm. long, truncate, ellipsoid, apparently green; calyx teeth 0.8–1.3 mm. long, deltoid, obtuse, thick foliaceous, hirsutulous; bud 18–20 mm. long, gently arcuate, the apex decurved at 55° from the axis of the ovary and corolla base; corolla in anthesis 22–25 mm. long, glabrous, curved subcylindric, at base 2–2.5 mm. in diameter, gradually slightly enlarging upwards to the throat where 3.5–4 mm. in diameter; proximal protruding knob 10 mm. from the base of the corolla, asymmetric conic, obtuse, pointed backwards, 1 mm. high, the two lateral knobs about half as large and slightly nearer the pale corolla base; the dorsal suture in late anthesis parted to the knob, so the tube only 10 mm. long; corolla 2-lipped; upper lip 2-lobed, the lateral sutures split down only 8–10 mm., the lobes strap-shaped, 1.7–1.8 mm. wide, abruptly narrowed to the obtuse tip, decurved below the column which is exserted through the upper suture; lower lip subequally 3-lobed, the sutures 7–9 mm. deep, the lobes 1.5–1.7 mm. wide, strap-shaped, abruptly contracted to the subacute tip, all corolla lobes sparsely papillose within; staminal column 17–21 mm. long, gently decurved, glabrous, pale; upper anthers 8–8.5 mm. long, glabrous; two lower anthers 6–8 mm. long, the apex penicillate,

the stiff hairs 1.5–2 mm. long, white; stigmas briefly short exserted (for 1–1.3 mm.), low rounded, with a central crease; ovary 1.5 mm. long, ellipsoid; berry 6–7 mm. in diameter, globose-turbinate, apophysate, greenish; seeds 1.4–1.5 mm. long, 0.7–0.9 mm. wide, 0.2–0.3 mm. thick, elliptic, flat, with strong wavy parallel transverse ridges, the eminences rounded or muriculate, the raphe forming a prominent, thickened, straw-colored margin, the flat faces dull brown, but the color in places masked by the pale epidermis.

HOLOTYPUS: Niihau, *W. T. Brigham* (distributed by *Mann & Brigham*), (BISH).

SPECIMENS EXAMINED: Kauai ou Nihau (=Niihau), 1851–55, *J. Remy 300 bis* (GH; and photo in BISH).

H. Mann, Jr., commented (1867: 180) on this Remy collection, "more probably Niihau —where it was also found by Mr. W. T. Brigham." Rock (1919*a:* 357) observed that, "The plants from Niihau collected by Remy are much more robust, the stems being nearly 5 cm. in diameter." The three sheets of the type collection, by Brigham, in the Bishop Museum, contain seven branches, all of them sections split longitudinally from the heavy and densely flowered stems. The longitudinal stem sectors were flattened in pressing, so that one cannot be sure of their original diameter. A revised estimate is 1–2 cm. at the base of the lowest leaves.

The occurrence of a *Delissea* on Niihau is very noteworthy, for the lobelias in general and all of the species of *Delissea* in particular, occur in moist forests, usually in the rainforest. That a *Delissea* was twice collected between 1850 and 1865 by different botanists is an indication of the occurrence then on the uplands of a moist forest. Brigham, then the director of the Bishop Museum, is quoted by Forbes (1913: 25) as saying, "this is the only *lobelia* that he saw on the island, and that it was more plentiful over the area where it occurred than perhaps any other lobeliaceous plant occurring in an equal area on the [Hawaiian] group." The species is certainly extinct now, having vanished when domestic grazing animals destroyed the native forest.

Delissea undulata, collected by Gaudichaud in 1819 was described by him (1829: 457 and pl. 78). His description in Latin consists of 12 words, only 9 of which are descriptive. His own type specimen, now in Paris, gives the locality Iles Sandwich. No more precise localization has been found. A photograph of his type specimen has been published by Rock (1919: 201) and this shows a specimen in fruit and flower, and with slender, linear-lanceolate blades, coarsely and irregularly sinuate dentate. Though with broader leaves, a collection by Hillebrand, August 1870, dry pali of Olualu (Olowalu) gulch, West Maui, was photographed by Rock when in Berlin and this excellent photograph is in the Bishop Museum. It is similar to the generalized drawing published by Gaudichaud (1826–30, Atlas: pl. 78). The plant has broader, less deeply lobed blades, but it appears to be of the same species, *D. undulata* Gaud., and it was so determined by Rock.

There is a *D. undulata* Gaud. var. *serrulata* Wawra, described from fruiting material, Wawra 1,943, from Waihee, Maui. Rock (1919: 353) reduced this to the synonymy of the species and cited Wawra's specimen which he had studied in Vienna. This may well belong in the synonymy of *D. undulata*, but in lack of flowers it cannot be placed with certainty. It appears, then, that the *D. undulata* Gaud. was probably collected by Gaudichaud in the adjacent mountains when the "Uranie" was anchored at Lahaina, Maui. *D. undulata* Gaud. has the blades linear-lanceolate, coarsely and irregularly sinuate-dentate, and apparently much larger, while *D. niihauensis* has the blades broadly ovate, crenate, and 5.5–7.5 cm. long.

D. fallax Hbd., apparently the closest relative, has the blades 7–23 cm. long, 2.3–5.8 cm. wide, narrowly elliptic, apiculate, serrate; petioles 3–13 cm. long; calyx lobes subulate, glabrous; corolla 15–17 mm. long, with a single, inconspicuous dorsal knob;

anthers 4.5–6 mm. long; penicillate brush 1–1.3 mm. long; berry 10–12 mm. in diameter. In contrast, *D. niihauensis* has the blades 5.5–7.5 cm. long, 3.4–5 cm. wide, broadly ovate, crenate; petioles 2–4 cm. long; calyx teeth deltoid, hirsutulous; corolla 22–25 mm. long, with one conspicuous dorsal and two lateral knobs; anthers 6–8.5 mm. long, the penicillate brush 1.5–2 mm. long; berry 6–7 mm. in diameter.

Rock (1919*a:* 353, 357) lists two of his own collections, 3,950 and 10,053, from the western side of the island of Hawaii, simple stalked trees more than 30 feet high, and relates his surprise at finding these on Hualalai, Puuwaawaa, and Pulehua. A similar specimen, *Forbes 263.H*, from Kanahaha, Kona, Hawaii, has recently been described as *Cyanea argutidentata* E. Wimm. Its only two mature flowers scarcely show the single gibbous corolla hump, but it is evident on the flowers of other collections of what is considered the same species, all from Kona, Hawaii: Puuwaawaa, *Rock 3,950;* Pulehua, Mauna Loa, *Rock 10,053*, and Kanehaha (=Kanahaha) *Forbes 264.H;* and Hanehane, *Forbes 196.H*. For the latter there is a drawing showing the single, proximal gibbous swelling at the apex of the corolla tube, and recording the swelling as red, while the lower part of the corolla as white, the upper part with reddish dots, the corolla lobes, filament tube apex, and stigmas pea green. Since this population has the technical characters, the following transfer is proposed.

Delissea argutidentata (E. Wimm.) comb. nov.

Cyanea argutidentata E. Wimm., Engler's Pflanzenreich IV, 276b(1): 75–76, fig. 21, 1943.

HOLOTYPE: Hawaii, "Wald unterhalb Koa Kanehaha-Kona, blühend im Juni (C. N. Forbes n. 263 H)" (BISH). This was a translation by Wimmer of the original data: Growing in the forest under koa, Kanehaha (=Kanahaha), Kona, June 26, 1911. J. F. Rock has subsequently redetermined Wimmer's species as *Delissea undulata* Gaud., reaffirming his opinion of the Hawaiian plants expressed in his monograph of 1919. That grouped the diverse plants of Kauai, Niihau, Maui, and Hawaii as one species. The writer here shows that the holotype was from West Maui, a plant having flowers with three gibbous humps; that the Kauai record is dubious; that the Niihau one is a new species, *D. niihauensis;* and that the one from Hawaii having calyx lobes 1–2 mm. long, and usually smaller, shorter leaves is still a different one, *D. argutidentata*. This latter is very close to *D. fallax* Hbd. from the Hilo region on eastern Hawaii, which is known only from the type collection and shows calyx lobes "about 3 mm. long." When more collections are found to represent *D. fallax*, its placement should probably again be re-examined. Concerning the other segregates, the evidence is more abundant, and the conclusions more certain.

A close examination of Forbes's field notebooks reveals that his no. *263.H* was an undetermined grass, and that no. *264.H* is the correct number of this collection of Lobeliaceae. Forbes himself made the correction on one sheet (BISH), but the duplicate sent to Wimmer went under the number *263.H*. Thus the holotypic collection of *D. argutidentata* should now read Kanehaha (=Kanahaha).

COMPOSITAE

Lipochaeta kawaihoaensis sp. nov. (§ Lipochaeta)

Fig. 9

NOM. VERN.: "ko'oko'olau."

DIAGNOSIS HOLOTYPI: Perennis suffruticosa erecta 3–8 dm. alta, corona pluri-ramifera, caulibus principalibus griseis deinde brunneis longitudinaliter sulcatis multi-ramosis in basi 2–7 mm. diametro, ramis lateralibus anguste pluri-angulosis adpresso-hispidulosis late divergentibus, petiolis 4–18 mm. longis gracili-

bus adpresso-hispidulis, laminis 1.2–4 cm. longis 7–28 mm. latis ovatis ad deltoideo-ovatis acutis vel obtusis firme crasse chartaceis et scabrissimis marginibus grosse crenatis vel etiam serratis supra obscure olivaceis in nervis adpresso-hispidis in intervallis adpresso-hispidulosis pilis cum basibus pustulatis infra pallide viridibus et adpresso-hispidulosis, capitulis terminalibus solitariis vel raro in ramulis parvis cum bracteis reductis et cymis elongatis 3-capitatis simulantibus, pedunculis 3–17 cm. longis nudis, involucris in flore 6 mm. altis 10–12 mm. diametro sed in fructu rotatis et subreflexis, phyllaris biseriatis viridibus crassis coriaceis 13-nervosis subacutis ellipticis vel lanceolatis extra et infra adpressi-hispidulosis, phyllaris exterioribus 5 et 4–8 mm. longis, interioribus 6–7 et simulantibus, receptaculo in flore lanceoloideo in fructu conico 4 mm. alto, paleis 5–6 mm. longis oblanceolatis scabris carinatis plurinervosis, floribus radiatis 6–9 luteis, laminis 7–9 mm. longis late ellipticis pluri-nervosis emarginatis et subtridentatis, tubo 1 mm. longo, setis pappi 3–5 inaequalibus 1–2 mm. longis linearibus vel oblanceo-linearibus crassis rigidis scaberulis eis majoribus canaliculatis, stylo 2 mm. longo filiformibus, stigmatibus 2 ligulatis 1.5–2 mm. longis, achaeneis juvenalibus 1.8–2 mm. longis 1.7–1.9 mm. latis trigonatis latere distali convexo late cuneiforme apice dense breve albo-hispiduli, achaeneis maturis 2.7–3.1 mm. longis 1.9–2.7 mm. latis trigonatis late cuneiformibus lateribus brunneis et nigro-maculatis forte tuberculatis apice subplanato luteo-hispiduloso, aristis 1.5–2 mm. longis subulatis adscendenti-hispidulosis subpersistentibus, floribus disci ca. 80, corollis 4 mm. longis luteis, tubo 1.5 mm. longo tubuloso, limbo anguste infundibuliforme 2.5 mm. longo 5-lobato, lobis 0.8 mm. longis deltoideis divergentibus, filamentis 1 mm. longis filiformibus pallidis, tubo staminalis 1.8 mm. longo in apice 0.5 mm. diametro ad basim attenuato, saccis antherae nigris, apicis connectivi pallidis deltoideo-ovatis, stylo 3 mm. longo pallido basi 0.4–0.5 mm. longo cylindrico subnigro firmo, stigmatibus 1 mm. longis ligulatis acutis, arista pappi unica ligulata subulata 2.1–2.3 mm. longa, achaeneis disci juvenalibus 1.8–2 mm. longis 0.7–0.9 mm. latis cuneiformibus compressis lateribus convexis glabris apice obliquo hispidulo, achaeneis disci maturis 2.5 mm. longis 1.7–2 mm. latis late cuneiformibus subluteis et pallide brunneo-maculatis in parte levibus in parte tuberculatis tetragonis basi obtusa vel truncata apice lato dense luteo-hispiduli marginibus tuberculatis, seta pappi plerumque una 1–2.3 mm. longa subulata hispidula curvata.

Perennial suffruticose, erect, 3–8 dm. tall; the crown bearing several branches; the main stems much branched, gray, becoming brown, longitudinally fissured, 2–7 mm. in diameter at base; the lateral branchlets sharply several-angled, appressed hispidulous; petioles 4–18 mm. long, slender, appressed hispidulous; blades 1.2–4 cm. long, 7–28 mm. wide, ovate to deltoid-ovate, acute or obtuse, thick, firm chartaceous and very scabrous, the margin coarsely crenate or even serrate, above dull olive green, appressed hispid on the veins, on the intervals closely appressed hispidulous from pustulate bases, below pale green and closely appressed hispidulous; heads terminal, usually solitary at tips of branches but rarely on small shoots with reduced bracts simulating an elongate 3-headed cyme; peduncles 3–17 cm. long, naked; heads heterogamous, radiate; involucre in anthesis 6 mm. tall, 10–12 mm. in diameter, but in fruit widespreading and rotate or somewhat reflexed; phyllaries in 2 rows, green, thick, coriaceous, with about 13 longitudinal nerves, subacute, broadly or narrowly elliptic or lanceolate, rough appressed hispidulous without and within, the outer ones mostly 5 in number, 4–8 mm. long, the inner ones 6–7, similar; receptacle in anthesis lanceoloid, in fruit conic, about 4 mm. tall and taller than broad; chaff 5–6 mm. long, oblanceolate, cartilaginous, rough scabrous, carinate, the back keeled, with numerous close longitudinal

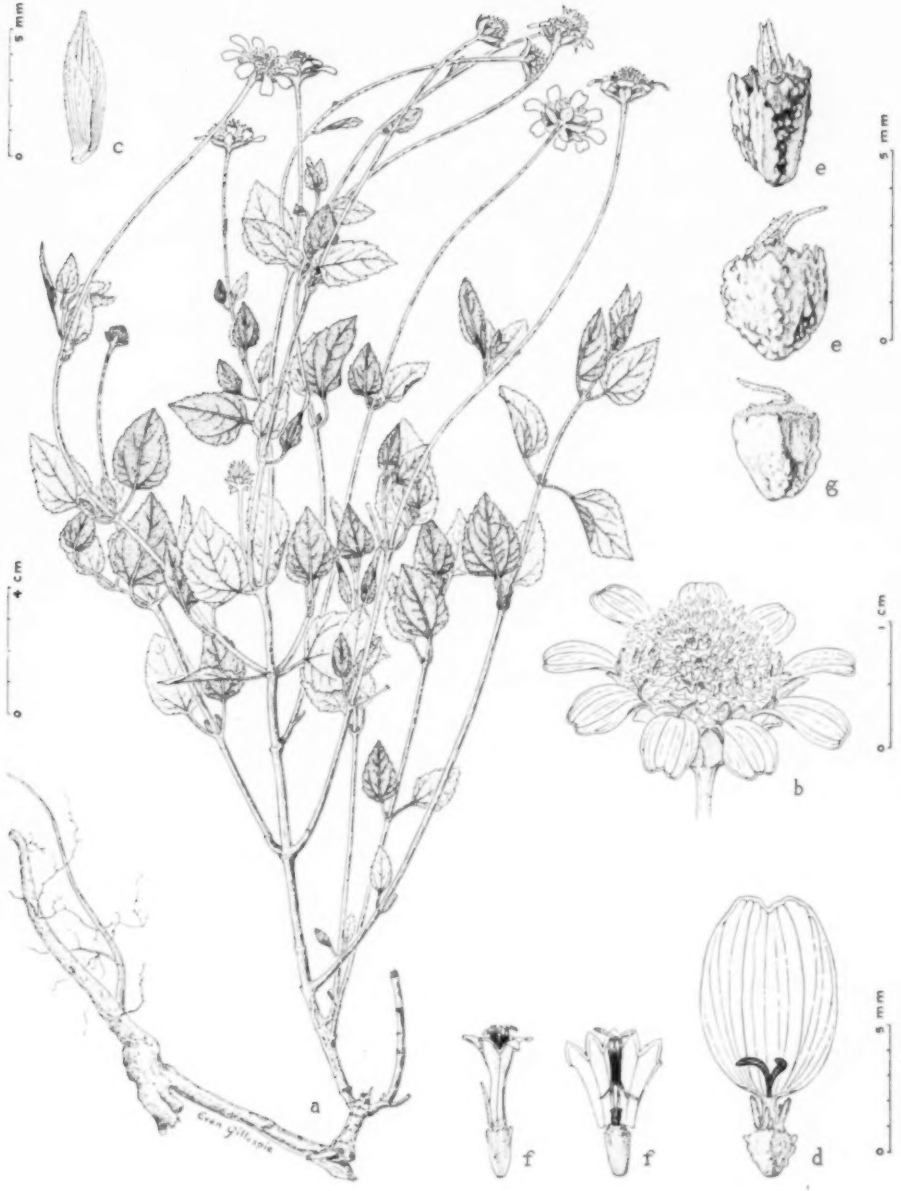

FIG. 9. *Lipochaeta kauaihoaensis*, from holotype: *a*, habit × ½; *b*, head × 2; *c*, chaff × 4; *d*, ray flower × 4; *e*, ray achene × 6; *f*, disk flower × 4; *g*, disk achene × 6.

parallel veins; ray flowers marginal, 6–9, bright yellow, the ray 7–9 mm. long, broadly elliptic, with numerous longitudinal parallel nerves, at apex emarginate and more or less 3-toothed; corolla tube 1 mm. long; pappus awns unequal, 3–5, and 1–2 mm. long, linear or oblance-linear, thick, rigid, ascending scaberulous, the larger ones channelled on the inner side; style 2 mm. long, filiform, the base not distended; stigmas 2, ligulate, 1.5–2 mm. long; the young ray achene 1.8–2 mm. long, 1.7–1.9 mm. broad, trigonous, and the broad distal face convex, broad cuneiform, the apex densely short white hispidulous; when mature the ray achenes 2.7–3.1 mm. long, 1.9–2.7 mm. wide, almost as thick, trigonous, broadly cuneiform, the sides brown, mottled with black and strongly tuberculate, the broad apex flatish or sloping, yellowish hispidulous, awns 1.5–2 mm. long, subulate, ascending hispidulous, several of them persistent; disc flowers about 80; disc corollas 4 mm. long, yellow, the tube 1.5 mm. long, tubular, the limb narrow funnel-form, 2.5 mm. long, 5-lobed, the lobes 0.8 mm. long, deltoid, spreading; filaments 1 mm. long, filiform, pale; staminal tube 1.8 mm. long, 0.5 mm. in diameter at apex, narrowing below, the linear anther sacs black, the apical connective tips pale, deltoid-ovate; style 3 mm. long, pale, springing from a dark firm style base 0.4–0.5 mm. long, cylindric, slightly tapering below, and with an expanded apical marginal rim; the 2 stigmas 1 mm. long, ligulate, acute; pappus of a single ligulate, subulate awn 2.1–2.3 mm. long, attached apically near the base of the corolla tube; the young disk achenes 1.8–2 mm. long, 0.7–0.9 mm. wide at apex, narrowly cuneiform and tapering downwards, compressed, the two sides convex, glabrous, the sloping apex densely hispidulous; disk achenes when mature 2.5 mm. long, 1.7–2 mm. wide, broadly cuneiform, yellowish, mottled with pale brown, partly smooth, partly low tuberculate, less thick than wide, but clearly tetragonal, the base obtuse or truncate, the apex broad, gently sloping, closely yellowish hispidulous, the margin with low tubercles, the usually single awn apical, 1–2.3 mm. long, subulate, ascending hispidulous, sharply bent.

HOLOTYPUS: Niihau, Kawaihoa Point, 300 ft. alt., in dry tuff, head of steep gully, erect, much branched shrubs, rays yellow, disk dark yellow, March 31, 1949, *H. St. John 23,611* (BISH).

This plant has been carefully compared with the known species and varieties of *Lipochaeta*. It is outstanding in the genus by having the receptacle at first lanceoloid, then ultimately conic, instead of flat or gently convex. It is most similar to *L. lobata* var. *denticulata* of the island of Oahu, but this variety has the petioles 2–5 (-9) mm. long; inner and outer phyllaries oval, subequal; chaff obtuse; ligulate flowers 8–18; and the achenes 2.9–3.6 mm. long, verrucose, sharply angulate, narrowly obdeltoid, compressed. *L. kauaihoaensis* differs from it by having the petioles 4–18 mm. long; the inner phyllaries lanceolate, longer and narrower than the outer ones; chaff acute; ligulate florets 6–9; and the achenes 2–3.1 mm. long, 1.7–2.7 mm. wide, the sides tuberculate, the angles not winged or margined. There is a lesser similarity in appearance to *L. tenuis* var. *Sellingii* of Puu Hapapa, Oahu, which variety is different in having the habit decumbent or suberect; blades oblong-lanceolate, at base broadly cuneate, the margin sharply serrate; peduncles 2–5 cm. long; disk flowers with corolla lobes equaling the tube, the pappus of 4 bristles as long as the corolla tube, and the achenes obovate, triangular with the angles more or less winged. On the other hand, *L. kauaihoaensis* can be known by having the habit erect; blades ovate to deltoid-ovate, at base rounded, the margin coarsely crenate or even serrate; peduncle 3–17 cm. long; disk flowers with corolla lobes ⅓ as long as the tube, pappus of a single ligulate-subulate awn slightly more than ½ as long as the corolla tube; achenes broadly cuneiform, tuberculate, not winged.

The new species is named from its only known locality, the volcanic, mountainous point at the south end of Niihau Island; to its name is added the Latin suffix, *-ensis*, indicating place of origin.

Lipochaeta lobata DC., var. ***incisior*** var. nov.

Fig. 10

L. lobata sensu C. N. Forbes, not of DC.

L. lobata DC. var. *Aprevalliana* sensu Sherff as to Niihau specimen, not of (Drake) Sherff.

NOM. VERN.: "nehe."

Foliis majoribus inciso-serratis lobatisque.

It has the larger blades incised serrate and lobed.

HOLOTYPUS: Niihau, Kaaliwai, in thicket with *Euphorbia celastroides* and *Artemisia australis*, 750 ft. alt., shrub 1–1.5 m. tall; leaves scabrous, chartaceous; involucre green; rays yellow, March 29, 1949, *H. St. John 23,572* (BISH).

SPECIMENS EXAMINED: Niihau, Kaali, January 1912, *J. F. G. Stokes*. This is an immature specimen, only 34 cm. tall, and with the blades lance-ovate, merely incised serrate, but it is from the same locality, has blades similar to the smaller ones on the holotype, and is certainly of the same variety.

The most similar variety to this new one is *L. lobata* var. *denticulata* of Oahu, which has the blades subentire to crenate-dentate or serrate, but not lobed. The new varietal name is from the Latin, *incisor*, more deeply cut.

Lipochaeta lobata DC. var. **maunaloensis** Sherff

L. lobata sensu C. N. Forbes, not of DC.

Niihau, south half of Island, January 1912, *J. F. G. Stokes*.

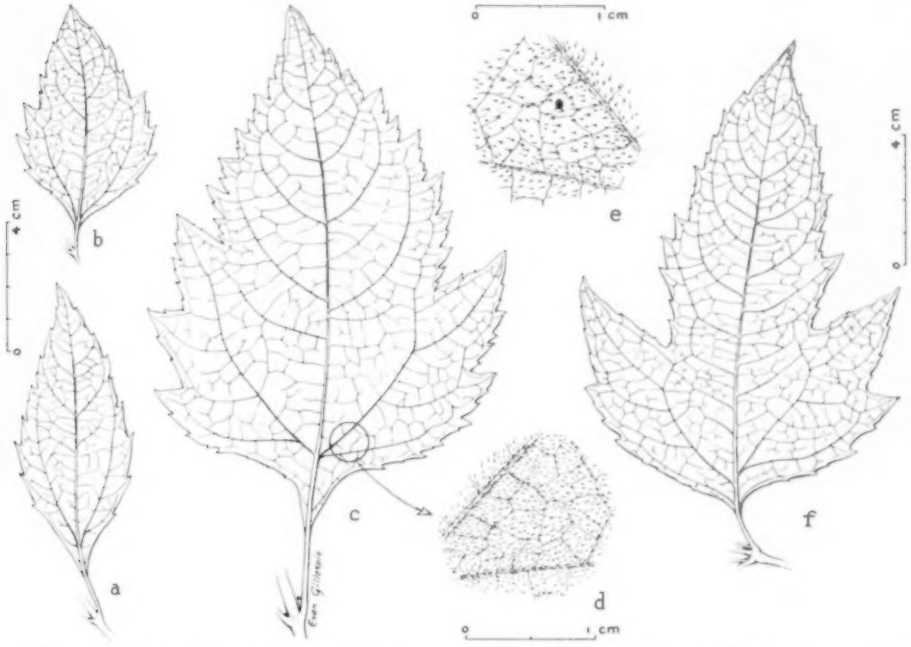

FIG. 10. *Lipochaeta lobata* var. *incisior*, from holotype: *a*, *b*, *c*, *f*, leaves × ½; *d*, lower leaf surface × 2; *e*, upper surface × 2.

This is a good flowering and fruiting specimen and it matches nicely the holotypic specimen from Mauna Loa, the dry end of Molokai. This Niihau specimen was not seen by Sherff.

Lipochaeta niihauensis, sp. nov.
(§ Lipochaeta)

Fig. 11

NOM. VERN.: "pa'apa'a'ina" (=crackle; probably in allusion to the stiff, brittle leaf blades).

DIAGNOSIS HOLOTYPI: Frutex 1 m. altus erectus ramosus, caulibus principalibus tertibus scabris, ramulis angulosis scabris et adscendenti-adpressi-hirsutulis, petiolis 4–20 mm. longis oppositis minime connatis et perfoliatis in apice basique dilatatis et adscendenti-albo-hispidulis, laminis 1.5–6.2 cm. longis 8–56 mm. latis crasse chartaceis sed rigidis et maxime hirsutulo-scabris et subadpresso-albo-hispidulis late ovatis in basi rotundatis vel subcordatis apice abrupte subacuti marginibus bisdentato-serratis infra pallidioribus proxime basi triplinervatis, capitulis in cyma laxa 3-capitata vel ita cum ramulis axillaribus tardis tenuibus cymis tricapitatis ferrentibus, pedunculis 1.5–6.5 cm. longis nudis dense subadpresso-albo-hispidulis, capitulis in flore cum involucro 4–5 mm. alto 8–10 mm. diametro sed in fructu patelliforme, phyllaris bi- (vel tri-) seriatis subviridibus exterioribus 5 (-7) subacutis 3–3.5 mm. latis late ovatis in marginibus et extra adpressi-hirsutulis firmis coriaceis 7-nervosis in basi carnosa, phyllaris interioribus paullo longioribus 2.5 mm. latis obovatis acutis, receptaculo in flore depresso-conico 1 mm. alto 2 mm. lato, paleis 3.5–5 mm. longo anguste cuneatis conduplicatis lateribus 0.8–1 mm. latis plurinervosis scariosis apicibus exsertis hispidulis, floribus radiatis marginalibus 8–14 in flore luteis, ligulis 8–9 mm. longis 3.8–4 mm. latis late ovalibus subtridentatis in latere distali valde bicostatis nervis gracilioribus 8, tubo 1.4 mm. longo aristis pappi plerumque 3 inaequalibus 0.6–0.9 mm. longis subulatis adscendenti-scaberulis, stylo 2.5 mm. longo, stigmatibus 0.7 mm. longis filiformibus, achaeneis radiatis juvenalibus 1.2–1.4 mm. longis trigonatis cuneiformibus in marginibus et apice hispiduli-ciliatis, achaeneis maturis 2.5–2.8 mm. longis 1.2–1.8 mm. latis valde trigonatis late cuneiformibus nigro-brunneis et griseo-maculatis ad apicem scabro-hispidulis ad basim ita diminuendibus ad basim marginibus lacero-alatis, aristis 3 (-4) inaequalibus 0.6–1.2 mm. longis subulatis, floribus disci ca. 100, corollis in flore viridi-luteis 4 mm. longis tubo 1 mm. longo cylindrico, limbo anguste infundibuliforme 0.9 mm. diametro 4-lobato lobis 0.5–0.6 mm. longis deltoideis adscendentibus, filamentis 1 mm. longis ligulatis pallidis, tubo staminalis 1.4 mm. longo 0.5 mm. diametro, sacis antheris subnigris apice connectivi pallidi deltoideo-ovati, stylo 3.5 mm. longo filiforme pallidi et basi 0.3 mm. longi cylindrici subnigri, stigmatibus 0.7–0.8 mm. longis ligulatis apice rhomboidei, aristis pappi binis 0.7–1.3 mm. longis subulatis barbellatis, achaeneis disci juvenalibus 1.3–1.9 mm. longis 0.6–0.8 mm. latis gracili-biconvexis cuneiformibus in marginibus et apice hispidulis, achaeneis maturis 2.8–3.2 mm. longis 1.1–1.7 mm. latis valde compressis et biconvexis medie vel anguste elliptico-obovatis basi obtusi apice truncati vel excavati brunneis et griseis maculatis ad apicem tuberculato-hispidulis marginibus cum alis membranaceis sive integris sive laceratis sive hispidulo-ciliato-laceratis, aristis binis 0.7–1.7 mm. longis aequalibus vel inaequalibus subulatis barbellatis in apice affixis.

DESCRIPTION OF ALL SPECIMENS: Shrub 1 m. tall, erect, with several branches; main stems terete, brown, scabrous from the remnants of pubescence; branchlets several-angled, roughened and ascending appressed hirsutulous; petioles 4–20 mm. long, opposite, connate and slightly perfoliate, dilated at base and apex, ascending white hispidulous; blades 1.5–9 cm. long, 8–77 mm. wide, thick chartaceous but stiff and very hirsutulous sca-

FIG. 11. *Lipochaeta niihauensis*, from holotype: *a*, habit × ½; *b*, head × 2; *c*, chaff × 4; *d*, ray flower × 4; *e*, disk flower × 4; *f*, ray achene, dorsal view, × 6; *g*, ray achene, lateral view, × 6; *h*, disk achene, dorsal view, × 6.

brous, and white subappressed hispidulous, broadly ovate, the base rounded or subcordate, the apex abruptly subacute, the margin doubly dentate-serrate, below a little paler, triplinerved from just above the base; heads in a loose, mostly 3-headed terminal cyme, or with 3-headed cymes on weak, late, lateral branchlets, peduncles 1.5–6.5 cm. long, naked, closely subappressed white hispidulous; heads heterogamous, radiate; involucre in anthesis 4–5 mm. tall, 8–10 mm. in diameter, but in fruit more widely spreading, knee-pan-shaped; phyllaries in 2 (or 3) rows, greenish, the outer ones 3–3.5 mm. wide, 5 (-7) in number, broadly ovate, subacute, appressed hirsutulous on the outer surface and the margin, firm coriaceous except at the firm fleshy base, 7-nerved; inner phyllaries slightly longer, 2.5 mm. wide, obovate, acute; receptacle in anthesis low conical, 1 mm. tall, 2 mm. broad; chaff 3.5–5 mm. long, narrowly wedge-shaped, the apex rounded to an acute tip, folded along the midrib, the sides 0.8–1 mm. wide, many nerved, scarious, the exposed tips hispidulous; ray flowers marginal, 8–14, when fresh yellow, the ray 8–9 mm. long, 3.8–4 mm. wide, broadly oval, shallowly 3-toothed at apex, on the distal side with 2 strong salient ribs from which the sides are infolded, weaker longitidunal ribs 8; ray corolla tube 1.4 mm. long; pappus awns mostly 3, unequal, 0.6–0.9 mm. long, subulate, ascending scaberulous; styles 2.5 mm. long; stigmas 0.7 mm. long, filiform; the young ray achenes 1.2–1.4 mm. long, trigonous cuneiform, the margins and apex hispidulous ciliate; when mature the ray achenes 2.5–2.8 mm. long, 1.2–1.8 mm. wide and nearly as thick, sharply trigonous, broadly cuneiform, dark brown, mottled with gray, towards the apex rough hispidulous and less so towards the base, the angles lacerate winged, awns 0.6–1.2 mm. long, 3 (or 4), unequal, subulate; disk flowers about 100; disk corollas when fresh greenish yellow, 4 mm. long, the tube 1 mm. long, cylindric, the limb very narrowly funnel-form, 0.9 mm. in diameter, 4-lobed, the lobes 0.5–0.6 mm. long, deltoid, ascending; filaments 1 mm. long, ligulate, pale; staminal tube 1.4 mm. long, 0.5 mm. in diameter, tapering downwards, the anther sacs blackish, the apical connective tips pale, deltoid-ovate; style 3.5 mm. long, filiform, pale, springing from a dark, cylindric style base 0.3 mm. long, with the upper rim expanded and lobed; the 2 stigmas 0.7–0.8 mm. long, ligulate with a narrowly rhombic tip; pappus of two subulate awns 0.7–1.3 mm. long, upward barbellate, attached above the lateral angles; the young disk achenes 1.3–1.9 mm. long, 0.6–0.8 mm. wide, thin biconvex, wedge-shaped, hispidulous on margins and apex; when mature the disk achenes 2.8–3.2 mm. long, 1.1–1.7 mm. wide, strongly compressed and biconvex, elliptic-obovate or narrowly so, the base obtuse, the apex truncate or excavate, the surface mottled brown and gray, the sides smooth towards the base, but upwards tuberculate hispidulous; each of the margins bearing a thin wing that is entire, lacerate, or hispidulous-ciliate lacerate; awns two 0.7–1.7 mm. long, equal or unequal, subulate, upwardly barbellate, attached apically.

HOLOTYPUS: Niihau, Kii, among rocks on basalt knoll, 100 ft. alt., April 2, 1949, *H. St. John 23,664* (BISH).

SPECIMENS EXAMINED: Niihau, Kii, between basalt boulders on rocky knoll, 75 ft. alt., April 2, 1949, *H. St. John 23,671*.

L. niihauensis is a member of the section *Lipochaeta* (*Microchaete*). Its closest relative is *L. subcordata* Gray var. *populifolia* Sherff of the island of Lanai, which variety is distinguished by having the stems 3–6 dm. tall; petioles 1–3 cm. long, slender; blades from narrowly ovate-cordate to lanceolate-cordate or narrowly deltoid, the principal ones broadly ovate, subcordate, the margins doubly sharply attenuate serrate; outer phyllaries about 4 mm. long; ray flowers 5–6, and 5–7 mm. long, their achenes 2–2.5 mm. long, 1.8–2 mm. wide, black, oblong-cuneate, trigonous, wingless, the apex truncate, the back with many high tubercles; disk corollas 3 mm. long,

narrowly funnelform, not contracted, pilosulous, their achenes 2–2.5 mm. long, 3-angled on the high convex back, giving a 4-angled appearance, the margins bluntly lobed or toothed, the sides high tubercled. *L. niihauensis* differs in having the stems 1 m. tall; petioles 4–20 cm. long, slightly dilated at base and connate; blades broadly ovate, the margins doubly dentate-serrate; outer phyllaries 5–6 mm. long; ray flowers 8–14, and the ray 8–9 mm. long, their achenes 2.5–2.8 mm. long, 1.2–1.8 mm. wide, dark brown mottled with gray, broad cuneiform, the angles lacerate winged, the apex crateriform, the back hispidulous; disk corollas 4 mm. long, cuneate-cylindric, contracted near the base, glabrous, their achenes 2.8–3.2 mm. long, thin biconvex wedge-shaped, the margins with a thin wing that is entire, lacerate, or hispidulous ciliate lacerate, the sides tuberculate hispidulous above but smooth towards the base.

The specific epithet is coined from the name of the island; and the Latin place ending, *-ensis*.

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Composition and Nutritive Value of Palolo (*Palola siciliensis* Grube)[1]

CAREY D. MILLER and FLORENCE PEN[2]

PALOLO is the Polynesian name of an annelid worm, which rises to the surface of the sea from the coral reefs of a number of tropical islands in the Pacific Ocean. For generations the native people have been able to predict the day and approximate hour in October and in November, which is their spring, when this swarming will take place. Sometimes it is November and December, or even later, as the time of the risings, both dates and hours, differs for the various locations and the phases of the moon.

According to Dr. Olga Hartman (1958), the annelid is designated *Palola siciliensis* (Grube) 1840, (=*Palola viridis* Gray, 1847). (In the past, the names *Eunice viridis*, *Eunice siciliensis*, and *Palolo viridis* have also been used.)

PALOLO IN THE SOUTH PACIFIC

The areas in the South Pacific Ocean where the palolo has been observed and where the natives have long used it as food have been reported by a number of scientists. Burrows (1955: 154) lists the following from the evidence which he has collected: "Fiji; Western Samoa; American Samoa; Tonga; Rarotonga (Cook Group), but not in the northern atolls; New Hebrides, but not in the three southern islands; Solomons, in a number of places."

The famous navigator, Mr. Harold Gatty,[3] who with Wiley Post flew around the world in 1931, and who collected the sample which we analyzed, was mainly interested in the "remarkable periodicity" of the rise. His investigations covered Samoa, the Fiji group, the New Hebrides, and the Solomons. In Fiji the worm is called "mbalolo," and in a letter dated January 21, 1954, Suva, Mr. Gatty wrote as follows:

From records over many years, there has been no deviation on the date of its two risings per year. If the last quarter of the moon is after the 15th of October, it will rise then and again on the last quarter of the moon in November, but if the last quarter of the moon is early in November, it will rise then and again on the last quarter of the moon in December. The rising is most exact on those days but only between the hours of four and eight a.m. The rising is usually continued on the next two succeeding mornings.

They (palolo) rise everywhere on and inside the reefs but are very few in numbers where they are in proximity to fresh or brackish water. The quantities that rise have to be seen to be believed. For instance, throughout the Fiji group there are actually many thousands of tons rising at the same instant. One can remain stationary either wading in shallow water, or anchored with a small boat in deeper water, and not fail to scoop up many pounds from any one spot.

In conversation with the senior author, Mr. Gatty stated in October, 1954, that the palolo rose not merely in thousands of tons, but, he estimated, in hundreds of thousands of tons.

COLLECTION OF PALOLO

Stair (1897: 142) describes collection of the palolo in November, 1843, near his residence on Upolu, Samoa, as follows:

"The worms are caught in small funnel shaped baskets, beautifully made, with handles about the centre. These baskets are skillfully glided over the surface of the ocean, and the worms emptied out as required into

[1] Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Technical Paper 413.

[2] Department of Foods and Nutrition, University of Hawaii Agricultural Experiment Station. Manuscript received February 4, 1958.

[3] Mr. Gatty died in Fiji, August 30, 1957.

another receptacle. When taken on shore, the worms are tied up in leaves in small bundles and baked. Large quantities are eaten uncooked, but, either cooked or uncooked, they are universally esteemed a great luxury. Such is the strong desire to eat palolo shown by all classes, that, immediately the fishing parties reach the shore, messengers are dispatched in all directions, bearing large quantities to parts of the islands on which none are found."

Buck (1930: 440) found that the coconut fiber scoops and those made from the coconut leaflet midrib were no longer in use in Samoa in 1927, as thin gauze or scrim which could be easily obtained from the traders made better scoops.

Figure 1, from photographs taken by Mr. Gatty in November, 1953, shows the Fijians collecting the palolo, using various kinds of homemade scoops, mostly of cloth. Since at this location the palolo start to rise about 4 o'clock in the morning, Mr. Gatty took these pictures as soon as it was light. When the sun rises, the worms disappear rather rapidly.

Kramer (1903: 405) observed that the rise of the palolo was an occasion for special feasts with singing, dancing, and general rejoicing among the Samoans.

NATURE OF PALOLO

Figure 2 shows broken specimens of the palolo. In the original fresh state, Wood-

FIG. 1. Natives collecting palolo in Fiji.

FIG. 2. Palolo showing eggs. About 5 × natural size.

worth (1907: 7) reports the longest one he measured was 30 centimeters (about 12 inches) in length, which is also "the average of the measurements given by seven authors." Our fresh-frozen specimens were 1 to 1½ millimeters in diameter. The females are filled with eggs, green in color, and the males with reddish-brown sperm. Since there are more females than males, the entire mass has a green color, resembling some of the edible sea weeds of the *Enteromorpha* species. In reality, the palolo which rises is the epitokal or long posterior end, i.e., the tail, of the worm. The head portion (atokal), which makes up about one fourth of the total length, stays in the coral rocks and generates a new body (Woodworth, 1907: 7).

Although marine biologists have been interested in the palolo for many years and the literature relating to taxonomy, morphology, and periodicity is extensive, the only chemical analyses we have found for *Eunice siciliensis* are those published by von Brand (1927: 688–691) as follows: dry matter, 31.19 per cent; ash, 2.94 per cent; and fat, 2.97 per cent.

PROCEDURE

Sample Analyzed

The sample of palolo analyzed was obtained by Mr. Harold Gatty on November 30, 1953, in the Fiji Islands. Immediately after it was collected it was placed in a refrigerator on his launch and taken to Suva where it was quick-frozen a little less than 24 hours after it was gathered. The day that a Pan American plane was due from the Antipodes on its way to Honolulu, a thermos jug containing the frozen palolo was flown in one of Mr. Gatty's planes from Suva to Nandy. At Nandy, it was kept in a refrigerator until placed on the Pan American plane (via Canton to Honolulu) and in less than 20 hours it was in our own freezer.

Analytical Methods

The methods used for the determination of

the approximate composition, minerals, and vitamins of palolo were the same as those previously outlined for pandanus (Miller, Murai, and Pen, 1956: 9).

RESULTS AND DISCUSSION

The composition of palolo is given in Table 1 along with a familiar protein food, raw beef round, for purposes of comparison. Although primitive people with a limited food supply usually make good use of all foods available, the enthusiasm of the Samoans and Fijians for palolo seems justified, as the analyses prove it to be a food of high nutritive value.

Palolo has 15 per cent of protein compared with about 20 per cent in beef; and the fat content is about half that of beef. Palolo has three times more calcium, about twice as much phosphorus, and about the same quantity of iron as beef. Beef would furnish no vitamin A or carotene, but palolo is an excellent source, having a greater vitamin A value than whole eggs. The thiamine content of both foods is low. Palolo has almost four times as much riboflavin as beef, but beef has almost four times as much niacin as palolo. Sufficient material was not available and we were not prepared to make analyses for additional vitamins or for amino acids.

TABLE 1
COMPOSITION OF PALOLO COMPARED WITH BEEF, PER 100 GRAMS

	PALOLO (raw)	BEEF (raw round)
Water, per cent	76.2	69.0
Protein, gm.	15.1	19.5
Fat, gm.	4.9	11.0
Crude fiber, gm.	0.78	0
Ash, gm.	2.42	1.0
Calcium, mg.	37	11
Phosphorus, mg.	310	180
Iron, mg.	2.9	2.9
Vitamin A, I.U.	514	0
Carotene, mcg.	1,350	0
Thiamine, mg.	0.07	0.08
Riboflavin, mg.	0.59	0.17
Niacin, mg.	1.3	4.7
Ascorbic acid, mg.	1.6	0

The palolo are eaten in the raw state just as they take them from the ocean; they are also eaten in the cooked state, and after cooking, they may be sun-dried to preserve them for future use. In Samoa the palolo are wrapped in leaves and cooked in the native oven of hot stones, often with coconut cream.

Mr. Gatty thought that palolo made the finest soup he had ever tasted and considered it warranted commercial exploitation as an Epicurean food. It is said to have a very delicious flavor, something like a cross between oyster and lobster, but superior to either.

Since palolo is a good protein food, rich in vitamin A, riboflavin, phosphorus, and iron, it seems unfortunate that it cannot be utilized to better advantage in the areas where it swarms. Because of the extremely short period when it can be gathered, the problem of reaping this nutritious harvest of the sea in any quantity will probably always remain a difficult one.

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Vegetative Anatomy of *Dubautia*, *Argyroxiphium*, and *Wilkesia* (Compositae)[1]

SHERWIN CARLQUIST[2]

BECAUSE *Dubautia*, *Argyroxiphium*, and *Wilkesia* are endemic Hawaiian genera of uncertain position within the Compositae and are characterized by species markedly different in habit, a more thorough knowledge of anatomical structure in these genera and in putatively related genera is desirable. The purpose of this study is to explore the variation pattern of anatomical characters in vegetative organs of *Dubautia*, *Argyroxiphium*, and *Wilkesia*, and to suggest which of these appear to be important in indicating relationships among the genera and to other genera. The data may also be helpful in outlining natural groups within the genus *Dubautia*.

Information concerning secondary xylem of *Dubautia* is included in a separate study (Carlquist, 1958). The peculiar leaves of *Argyroxiphium*, and comparison of them with leaves of *Wilkesia*, form the subject of an earlier paper (Carlquist, 1957*d*). The present paper concerns the vegetative anatomy of the three genera in other respects. For the purposes of this study, the writer interprets *Dubautia* as including *Railliardia*, a treatment offered by Keck (1936: 24–28) and accepted by St. John (1950).

The dubious position of *Dubautia* can be appreciated by comparing the works of authors who have dealt with the genus. Although recent authors agree that *Dubautia* and *Railliardia*, if both genera are recognized, are closely related, earlier authors recognized both genera and relegated them to widely separated portions of the family. Bentham and Hooker (1873: 393), for example, place *Dubautia* near *Argyroxiphium* and *Wilkesia*, whereas they locate *Railliardia* (*loc. cit.*, p. 442) between *Railliardella*, a genus traditionally placed in Senecioneae, and the Juan Fernandez Senecioneae *Robinsonia* and *Rhetinodendron*. Although the systematic positions of *Argyroxiphium* and *Wilkesia* have been in doubt, they have been interpreted as belonging to the tarweeds (Heliantheae, subtribe Madinae) by such authors as Hoffmann (1890: 248). Hoffmann, however, places *Dubautia* and *Railliardia* in the subtribe immediately preceding Madinae, Galinsoginae. Skottsberg (1931: 56; 1956: 211) finds *Dubautia* and *Railliardia* possibly related to *Robinsonia* and *Rhetinodendron*, as well as to a New Guinea genus of Senecioneae, *Brachionostylum*. Keck (1936: 8) agrees, although he emphasizes the relation of *Dubautia* to *Argyroxiphium* and *Wilkesia*, which he excludes from Madinae and places in Galinsoginae; and he suggests that *Dubautia* (*sensu lato*), *Argyroxiphium*, and *Wilkesia* form a related endemic group. The fact that he relates *Dubautia* to elements of both Heliantheae and Senecioneae is not incongruent, in his opinion, because *Dubautia* may be regarded as a genus transitional between the tribes. *Dubautia*, therefore, would seem to be a critical genus in the delimitation of the tribes of Compositae. St. John (1950: 240) finds no genus with close affinities to *Dubautia*, and Sherff (1935) declines to comment. Because the Heliantheae mentioned above are American, demonstration of relationship between them and *Dubautia*, *Argyroxiphium*, and *Wilkesia* would be important by validating an example of Hawaiian-American phytogeographical affinity.

MATERIALS AND METHODS

The author's collections (listed below) from which portions were preserved in Carnoy's Fluid (3 parts absolute ethyl alcohol:

[1] Manuscript received November 20, 1957.

[2] Claremont Graduate School, Rancho Santa Ana Botanic Garden, Claremont, California.

1 part glacial acetic acid) provided good material for anatomical study. The others of the species, however, were studied from fragments of herbarium specimens treated according to techniques described earlier (Carlquist, 1957*a*: 207). The liquid-preserved material was prepared by means of techniques described in that paper. Preparations made from herbarium material, both as whole mounts and as sections, gave quite satisfactory information concerning vegetative anatomy. Every effort was made to secure mature leaves, to analyze structure of several portions of a leaf, and to secure stems both in primary condition, for a study of stem structure, and with some secondary growth, for study of mature pith types. Pith of the rosette species of *Argyroxiphium* (*A. sandwichense*) was taken from basal (epicotyl) portions of the rosette. Leaf anatomy was studied in all species except *D. coriacea* (Sherff) Keck, *D. demissifolia* (Sherff) Keck, and *D. kohalae* (Skottsb.) St. John. These species would probably add little to the gamut of variation presented here. Stem anatomy was studied for the majority of the species of *Dubautia* and *Argyroxiphium*, as well as for *Wilkesia*. Subspecific variation was disregarded in this study, and analysis of the hybrids recognized by Sherff (1935) did not seem feasible at present.

Dubautia arborea (Gray) Keck, Rock 8344 (UC); *D. ciliolata* (DC.) Keck, var. *laxiflora* (DC.) Keck, Rock 10326 (UC); *D. Hillebrandii* (H. Mann) Keck, Hillebrand s.n. (GH, syntype); *D. Knudsenii* Hillebr., Carlquist H15 (UC); *D. laevigata* Gray, Heller 2616 (UC); *D. latifolia* (Gray) Keck, Heller 2887 (UC); *D. laxa* H. & A., Carlquist H12 (UC); *D. linearis* (Gaud.) Keck, Rock 8123 (UC); *D. lonchophylla* (Sherff) Keck, St. John 10303 (UC); *D. magnifolia* Sherff, Rock 9012 (BISH); *D. Menziesii* (Gray) Keck, Carlquist H17 (UC); *D. microcephala* Skottsb., Carlquist H14 (UC); *D. molokaiensis* (Hillebr.) Keck, Forbes 86Mo (UC); *D. montana* (H. Mann) Keck, Rock 8594 (UC); *D. paleata* Gray, Forbes 914K (BISH); *D. plantaginea* Gaud. var. *platyphylla* Hillebr., Carlquist H20a (UC); *D. platyphylla* (Gray) Keck, Forbes 1101M (UC); *D. railliardioides* Hillebr., Carlquist H16 (UC); *D. reticulata* (Sherff) Keck, Rock 8573 (UC); *D. Rockii* (Sherff) Keck, Rock 8601 (BISH); *D. scabra* (DC.) Keck, Carlquist H20 (UC); *D. Sherffiana* Fosb., St. John 23924 (BISH); *D. struthioloides* (Gray) Keck, Wilkes Exped. s. n. (GH, type); *D. ternifolia* (Sherff) Keck, Forbes 1175 (BISH); *D. thyrsiflora* (Sherff) Keck, Forbes 1203M (GH); *D. waialealae* Rock, Rock Oct. 1911 (GH, cotype). *Argyroxiphium Caliginii* Forbes, Carlquist H28 (UC); *A. Grayanum* (Hillebr.) Degener, Carlquist H27 (UC); *A. sandwichense* DC., Carlquist H19 (UC); *Wilkesia gymnoxiphium* Gray, Carlquist H10 (UC).

Gratitude is expressed to the curators of these herbaria for use of their materials. Data concerning the stem of *D. platyphylla* were obtained from a slide (prepared from a liquid-preserved collection by Degener, no. 19188) kindly given to the writer by Dr. John W. Hall. Thanks are due Dr. Harold St. John for his assistance during the author's field work in the Hawaiian Islands.

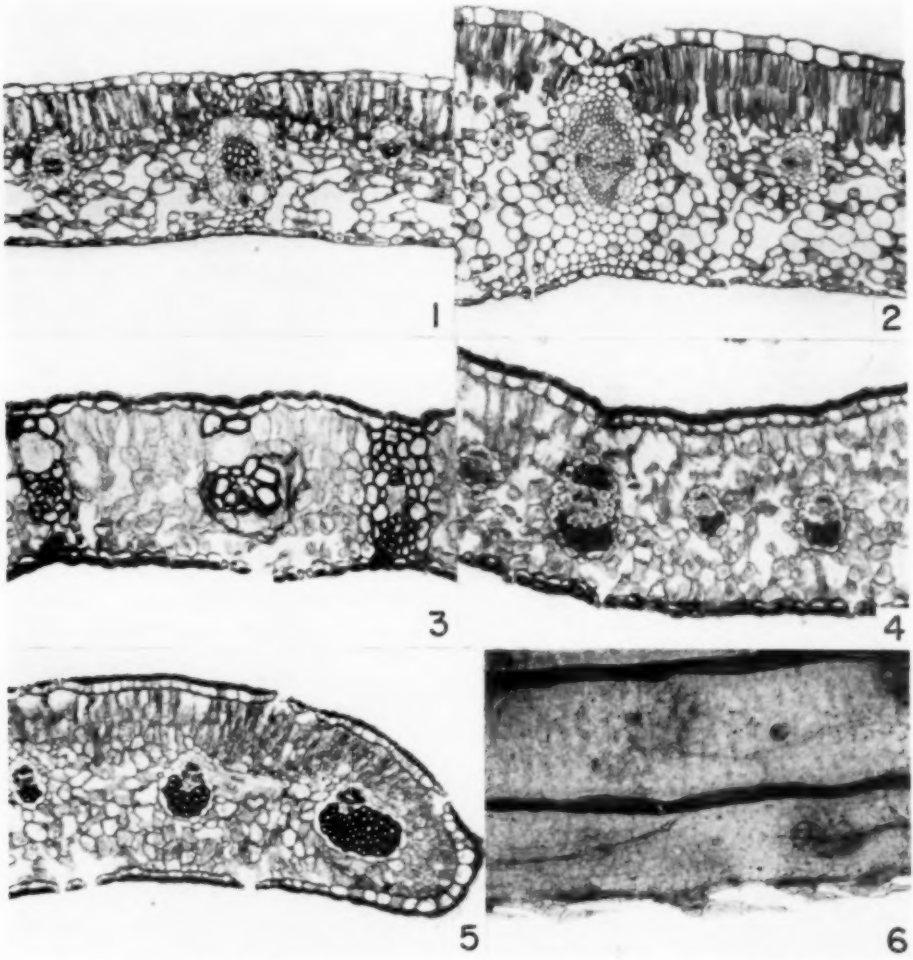
ANATOMY

Leaf Transections

Characters of leaf anatomy as seen in transections constitute the best indications of specific diversity in *Dubautia*. These characters include bifacial or isolateral organization, relative size of cells in upper and lower epidermis, thickness of cell walls in epidermis, width of palisade, frequency of bundle-sheath extensions, presence of fibers within the bundle sheath, presence of secretory canals in the bundle sheath, and occurrence of uniseriate nonglandular or biseriate glandular hairs. Cuticle is not included in description of epidermis cell wall thickness, because it was invariably a very thin layer. Numerous preparations showed separation of the cuticle from the epidermis (e.g., Fig. 3). The species of *Dubautia* are compared below by reference to "types" based on the species illustrated. No

taxonomic significance is necessarily implied by this arrangement. The groups below, however, do appear to be natural groups in some instances. For each group, the illustrated species is used as a basis for description, and the species most closely resembling it are listed beneath, with the features by which they differ mentioned in parentheses.

1. *D. Knudsenii* (Fig. 1). Leaf bifacial; cells of upper epidermis larger than those of lower epidermis, thin walled; 1 layer of palisade present; bundle-sheath extensions present on major veins only; fibrous bundle cap present only on major veins; secretory canals 4 near larger veins, 1 or 2 near smaller veins; trichomes absent at maturity.



FIGS. 1–6. Leaves of *Dubautia*. (1–5) Leaf transections. (1) *D. Knudsenii*, × 75. (2) *D. railliardioides*, × 67. (3) *D. latifolia*, × 95. (4) *D. waialealae*, × 87. (5) *D. Menziesii*, × 67. (6) *D. lonchophylla*, portion of cleared leaf to show marginal trichomes, below, and secretory canals, which appear as darker lines (on account of resins) beside two larger veins, × 58.

Like *D. Knudsenii:*

D. laxa (a few uniseriate hairs on lower surface).

D. molokaiensis (thicker outer walls on upper epidermis).

D. reticulata (thick-walled upper epidermis; uniseriate hairs frequent on both surfaces, especially in the grooves overlying veins on the upper surface).

2. *D. railliardioides* (Fig. 2). Leaf bifacial; cells of upper epidermis larger than those of lower epidermis; prominent grooves on upper surface above major veins; 2 palisade layers present; sheath extensions present on many larger veins; fibers common at both poles of larger veins; 4 secretory canals in outer portion of bundle sheath of larger veins, 1 or 2 near smaller veins; scattered uniseriate trichomes on lower surface and margins (upwardly appressed).

Like *D. railliardioides:*

D. magnifolia, D. microcephala, D. plantaginea (virtually identical with *D. railliardioides*).

D. paleata (sheath extensions on major veins only: fibers more common at phloem pole of veins; secretory canals absent; numerous uniseriate hairs on both surfaces).

D. ternifolia (fibers more common on phloem face of bundles).

D. scabra, D. ciliolata, D. lonchophylla, D. linearis, D. Sherffiana, D. thyrsiflora (upper epidermis very large celled; bundle-sheath extension on midvein only; fibers mostly on phloem face of bundle; usually 1 secretory canal above xylem pole of larger veins).

D. platyphylla (fibers at phloem face of bundles only; secretory canals absent; biseriate glandular hairs with large multicellular capitate heads and long stalks abundant on both surfaces; uniseriate hairs absent).

3. *D. latifolia* (Fig. 3). Leaf bifacial, thin; upper and lower epidermis cells of approximately the same size, very thick walled; a single layer of cells weakly defined as palisade; bundle-sheath extensions frequent, consisting of isodiametric to fiber-like sclereids, although no "bundle cap" fibers are present on the vascular bundles: 1 or 2 secretory canals present within the bundle sheath or sheath extension of many veins; hairs absent at maturity.

Like *D. latifolia:*

D. laevigata (sclerenchyma of bundle sheaths and sheath extensions consisting of thick-walled fibers; secretory canals absent).

4. *D. waialealae* (Fig. 4). Leaf bifacial; cells of upper and lower epidermis of about the same size, very thick walled; 1 or 2 layers somewhat differentiated as palisade; sheath extensions present only on midvein; prominent strands of thick-walled fibers on phloem face of veins, also on xylem pole of larger veins; secretory canals absent; large uniseriate trichomes abundant on upper surface and on margins.

5. *D. Menziesii* (Fig. 5). Leaf somewhat isolateral (stomata frequent on upper surface; adaxial palisade cells short, nearly isodiametric; cells on abaxial face like adaxial palisade cells in shape, with more numerous chloroplasts than cells in the central portion of the leaf); leaf very thick; bundle-sheath extension only on midvein; large groups of fibers on phloem face of veins (a few fibers on xylem pole of larger veins); secretory canals infrequent, 1 or 2 in bundle sheath of larger veins near leaf base; thick-walled uniseriate trichomes scattered over both surfaces and margin of leaf.

Like *D. Menziesii:*

D. Hillebrandii (nearly identical with *D. Menziesii*).

D. arborea (fibers lacking near veins; biseriate glandular hairs present on both leaf surfaces).

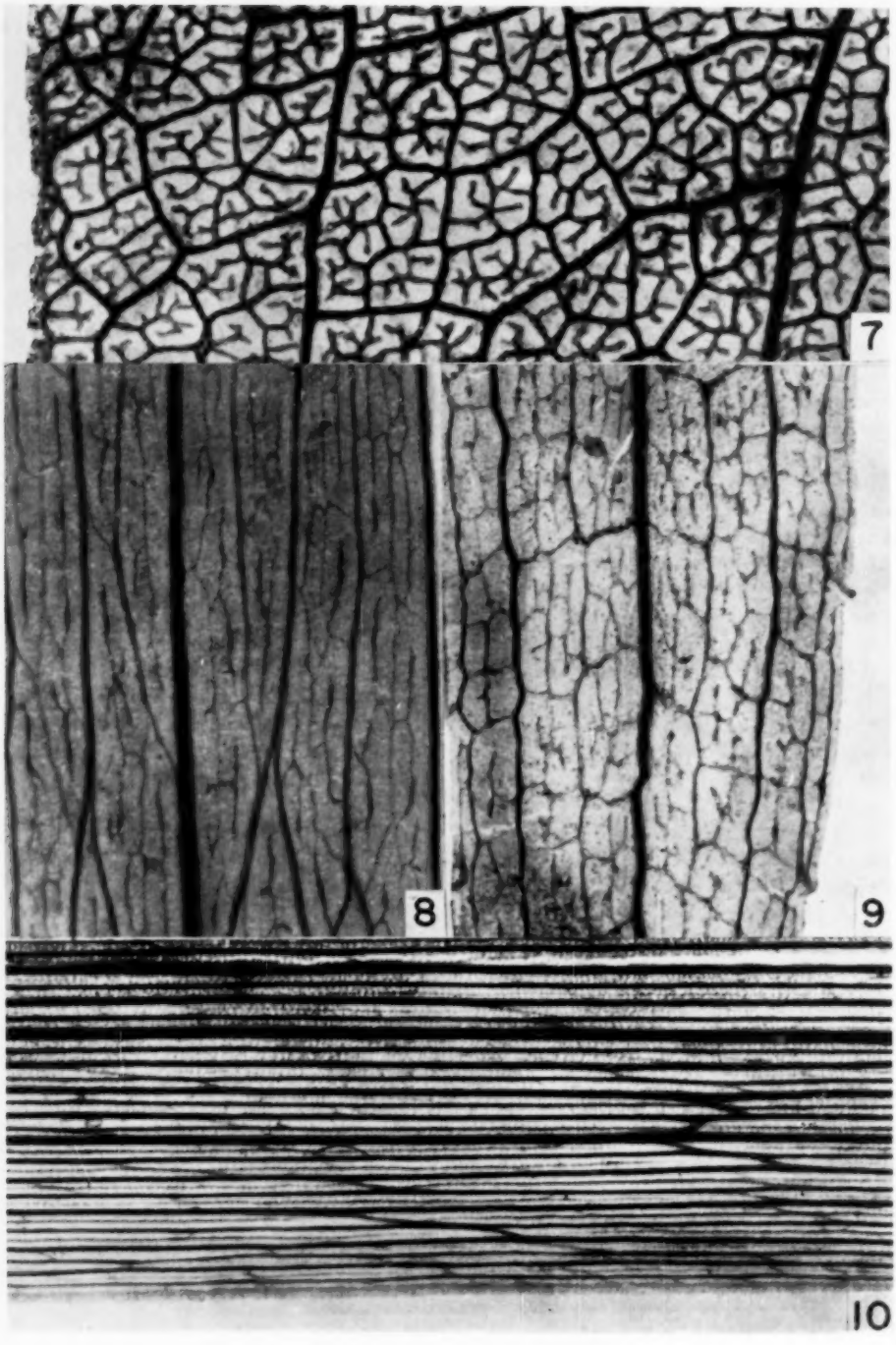
D. Rockii (a single secretory canal adaxial to most veins).
D. montana (fiber strands near veins small).
D. struthioloides (more nearly isolateral than *D. Menziesii*).

The different types of leaf structure detailed above reflect ecological conditions for *Dubautia* to a certain extent, as well as being indicative of taxonomic groupings. The thin, glabrous leaves of *D. Knudsenii*, with thin-walled epidermal cells, correspond to the moist forest areas on Kauai where that species grows. On the contrary, the tendency toward thick, isolateral leaves with thick-walled epidermal cells in *D. Menziesii* seems related to the dry, sunny alpine habitat of this plant. Most of the species indicated here as having similarity to *D. Menziesii* are also alpine types.

The highly specialized leaf anatomy of *Argyroxiphium* (Carlquist, 1957*d*) bears little superficial resemblance to that of even the isolateral-leaved species of *Dubautia*. The presence of fiber strands along veins, secretory canals (in *A. Caliginii*), and the presence of uniseriate hairs (much more abundant in *Argyroxiphium*) are similar features. The capitate biseriate glandular hairs on inflorescence bracts of *Argyroxiphium* and *Wilkesia* are very similar to those on leaves of *Dubautia platyphylla*. *Dubautia* shows little differentiation of leaves near inflorescences into inflorescence bracts, whereas in *Argyroxiphium* a marked difference, reflected in the anatomical structure, is seen between vegetative leaves and bracts of the inflorescence. The leaf of *Wilkesia*, which differs markedly from that of *Argyroxiphium* (Carlquist, 1957*d*), appears much like the leaf of *Dubautia laevigata* in transection. Although the genera *Dubautia* and *Wilkesia* lack the intercellular deposition of pectic compounds which is characteristic of *Argyroxiphium*, cell walls in leaves of *Dubautia* and *Wilkesia* are rich in pectic compounds. Treatment of leaves of the latter with hydrofluoric acid prior to sectioning proved impracticable because the acid released such compounds from the wall and caused swelling and distortion of the leaves. The phenomenon described by the writer as "abaxial meristem" in *Argyroxiphium* is totally lacking in *Dubautia*, as it is in *Wilkesia*.

Leaf Venation

Figures 7–9 show the range of venation types which may be seen in the genus *Dubautia*. *Dubautia latifolia* (Fig. 7) is exceptional for the genus in its reticulate vein pattern with polygonal areoles containing numerous freely-terminating veins. Except for the major veins (two of which are shown, left and right of center, respectively), there is no tendency for orientation of veins longitudinally in the leaf. *D. latifolia* is apparently the only species which has this venation pattern. This distinctive feature is recognized by the segregation of *D. latifolia* as a separate section of the genus, "*Venoso-reticulatae*" (Sherff, 1935: 111), whereas the remainder of the *Railliardia* species are included by Sherff in the section "*Nervosae*." The most typical venation condition in *Dubautia* is illustrated by *D. linearis* (Fig. 9). In this species, the five main veins run the length of the leaf, as in *D. latifolia*. Marginal veins and those between the primary veins also have a distinctly longitudinal course. Areoles are more nearly rectangular, elongated with the long axis of the leaf. Vein endings are frequent. *Dubautia microcephala* (Fig. 8), *D. plantaginea*, and *D. railliardioides* show a modification of this pattern. In these species all of the major venation and much of the minor venation show a longitudinal orientation. Areoles are very elongate, and vein endings are more infrequent than in *D. linearis*. The predominant pattern of venation in the genus *Dubautia*, then, is like that of *D. linearis*, and is therefore a departure from typical reticulate dicotyledonous venation. One may question whether the reticulate venation of *D. latifolia* is a primitive condition or a "reversion." The advanced position of *D. latifolia* in characters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other than venation may suggest the latter interpretation. Probably the type of venation shown by *D. linearis* is basic for the genus because it is found in conjunction with other unspecialized characters in some of the putatively primitive species. The type of venation illustrated by *D. microcephala* seems clearly a specialized condition.

Comparison of leaf venation in *Dubautia* with that of *Argyroxiphium* and *Wilkesia* is pertinent in this regard. Paradermal sections of *Argyroxiphium* leaves reveal that the basic venation is similar to that of *D. linearis* if the additional vein series denoted by the writer as "upper" and "lower" sets of veins (Carlquist, 1957*d*) are disregarded. *Wilkesia* (Fig. 10), on the contrary, is markedly different from *Argyroxiphium* in its venation. This remarkably monocotyledonous venation pattern is characterized by longitudinal orientation of virtually all of the major and minor veins. Cross-connections between the longitudinally oriented veins are infrequent. Although this pattern appears to be anomalous in comparison with the types described above, it may well have been derived from a type like that of *Dubautia microcephala* by means of a more nearly exclusive production of longitudinally oriented veins. Venation similar to that of *Wilkesia* has been described for another member of Compositae in *Schlectendalia luzulaefolia*, a member of the tribe Mutisieae (Urban and Möbius, 1884).

Nodal Anatomy

The genus *Dubautia* is curious because of the variation in phyllotaxy and the presence of both petiolate and sessile clasping leaves within the genus. Both of these characters of leaf attachment are related to the vascular pattern of nodes. Although the author's material did not prove sufficient for placing each species in a category, the data below probably indicate the full range of types which occur in the genus. The types indicated include all that have been reported previously for the family, except for multilacunar nodes with an alternate-leaved condition. This latter type does not occur in any of the alternate-leaved species, which are uniformly trilacunar. As some of the examples below show, transitions between the recognized types may occur in a single stem.

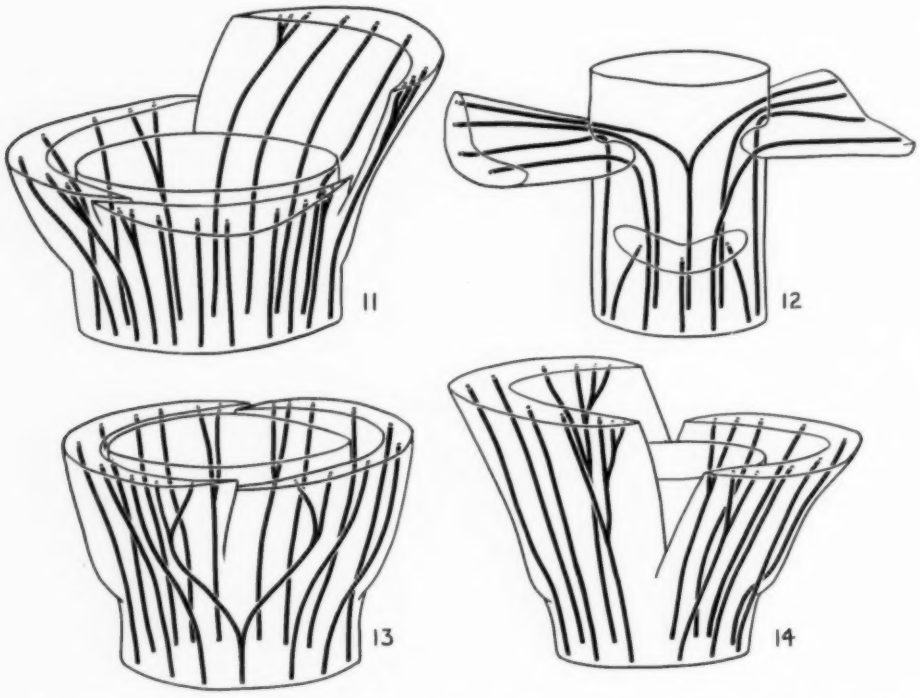
1. Trilacunar, alternate leaves. Examples: *D. Sherffiana*, *D. lonchophylla*.
2. Trilacunar, opposite (decussate) leaves. Examples: *D. Menziesii* (Fig. 12), *D. montana*, *D. latifolia*, *D. platyphylla*, *D. scabra*. The drawing of *D. Menziesii* shows, below, a trilacunar node with only the traces of the facing leaf indicated. Above is a node in which both leaves of the pair are supplied by 4 traces. This node, then, is transitional between trilacunar and multilacunar. The additional pair of traces, on the far side of the stem, fuse to a single trace a short distance below the node. Such fusion of adjacent laterals is not characteristic of trilacunar nodes in *Dubautia*.
3. Trilacunar, verticillate leaves. Examples: *D. ternifolia*, *D. waialealae*. The 3 traces of each leaf at a node continue downward into the vascular cylinder without fusion of adjacent laterals.
4. Multilacunar, opposite (or decussate) leaves. Examples: *D. laxa* (Fig. 14), *D. laevigata* (Fig. 13), *D. magnifolia*, *D. Knudsenii*. As comparison of Figures 13 and 14 shows, multilacunar nodes can differ in number of traces and in the fusion of traces below a node. In *D. laxa* (Fig. 14), each leaf is provided with 5 (or 6) traces, which continue downward into the vascular cylinder independently. The most lateral traces in each leaf base increase the number of veins in the leaf margin by branching toward the margin. In *D. laevigata* (Fig. 13), more numerous traces con-

FIGS. 7–10. Portions of cleared leaves to show venation. (7) *D. latifolia;* margin at left; × 10.5. (8) *D. microcephala*, × 13.5. (9) *D. linearis;* margin at right; × 9.5. (10) *Wilkesia gymnoxiphium;* margin below; × 9.5.

tinue downward into the vascular cylinder. In addition, the most lateral pair shown on the near side of the stem unite. This union of adjacent laterals, mentioned above for *D. Menziesii*, is characteristic of some Heliantheae with opposite leaves, and has been reported by Carlquist (1957*c*) for *Fitchia* and *Oparanthus*.

5. Multilacunar, verticillate leaves. Example: *D. railliardioides* (Fig. 11). Five traces, related to 5 gaps, enter each leaf at a node, which usually consists of 3 leaves. As in *D. laxa* and *D. laevigata*, increase in number of veins at the leaf base is accomplished by branching of the laterals. The occurrence of a multilacunar condition at a verticillate node is of particular significance because, according to Dr. I. W. Bailey (personal communication), this condition has never been reported in dicotyledons. The author (1957*d*) suggested that it may occur in *Argyroxiphium Grayanum*, a species which was demonstrated to have alternate leaves with multilacunar nodes, but in which rare individuals have verticillate leaves.

The great diversity of nodal types in *Dubautia* is of considerable interest. Despite this diversity, however, a marked contrast with *Wilkesia* occurs in regard to branching of veins in the leaf base. *Wilkesia* has verticils of numerous leaves, each of which is related to a trilacunar condition (Carlquist, 1957*d*, fig. 18). At the leaf base, the laterals are at the



FIGS. 11–14. Reconstructions of nodes of *Dubautia* (based on serial sections). (11) *D. railliardioides*, × 6. (12) *D. Menziesii*, × 11.5. (13) *D. laevigata*, × 5.6. (14) *D. laxa*, × 6.5. Darker lines represent veins; lighter lines represent the outlines of a nodal segment including leaf bases.

margins of the leaf and branches are given off toward the margin, whereas in *Argyroxiphium* the branches are given off toward the midveins. *Dubautia* resembles *Wilkesia* in this respect. In *Argyroxiphium* (Carlquist, 1957*d*, fig. 17), however, the alternate leaves are related to multilacunar nodes, and adjacent laterals of successive leaves in the spiral are united below the leaf base.

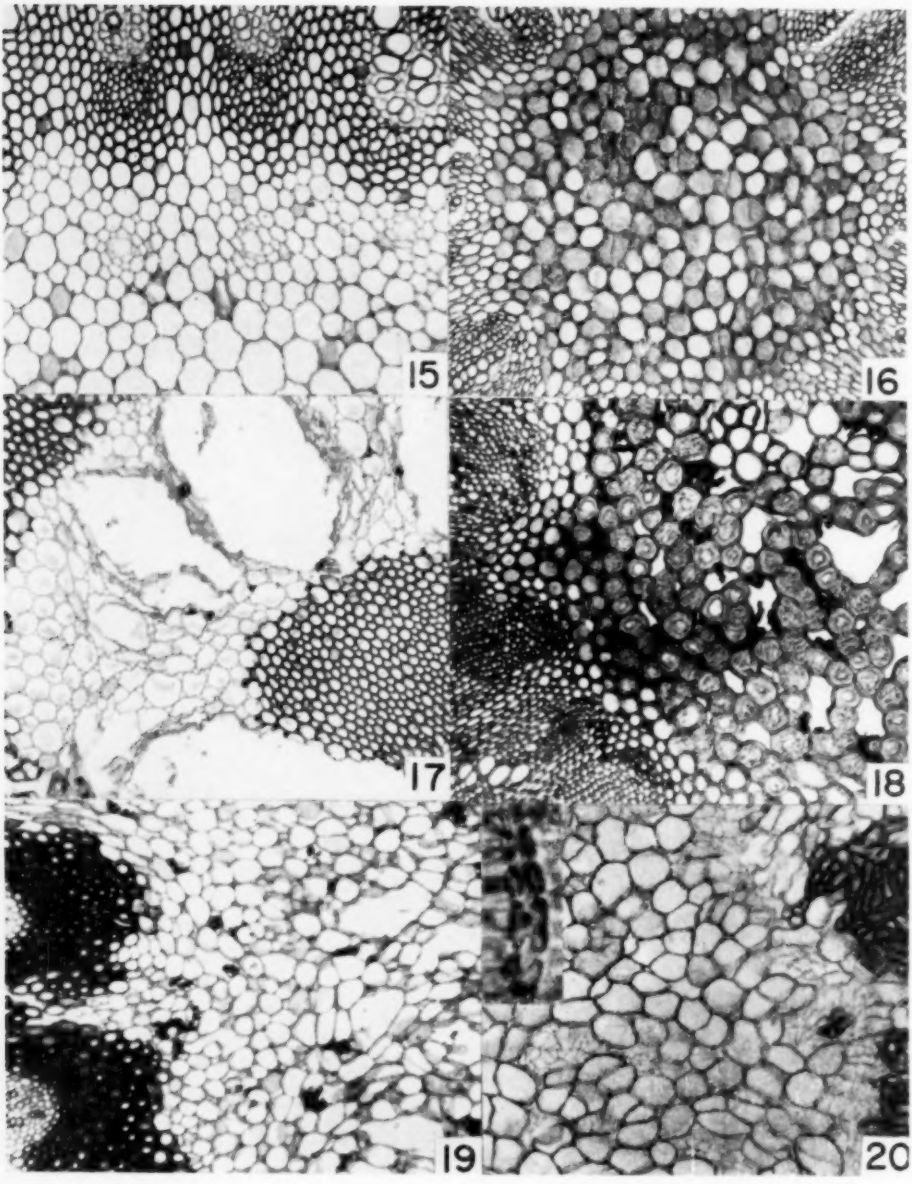
Dubautia, *Argyroxiphium*, and *Wilkesia*, then, are amply distinct from each other in nodal anatomy. The taxonomic interest of the different types within *Dubautia* seems evident; the phylogenetic relationship of the various types in the three genera, however, will be better understood when greater knowledge of nodal anatomy in Compositae at large is available.

Pith

The wide range of pith types in *Dubautia* is suggested by comparison of Figures 15–18 (see also Figs. 21, 22, right). As with patterns of leaf construction, these can be referred to a number of types; these should not be regarded as categories, however, although some reflect natural assemblages of species:

1. *D. plantaginea* (Fig. 15). Pith cells thin walled with small intercellular spaces; periphery (inner margins of bundles) sclerified; secretory canals present (opposite inner faces of larger bundles); no carbonized resin deposits present.
   Like *D. plantaginea:*
   D. microcephala, *D. railliardioides*, *D. lonchophylla* (virtually identical with *D. plantaginea*).
   D. paleata (peripheral sclerenchyma very thick walled).
   D. scabra (secretory canals infrequent).
   D. magnifolia (periphery unsclerified).
   D. ternifolia (patches of sclereids present throughout pith).
   D. Knudsenii, *D. platyphylla*, *D. laxa*, *D. ciliolata* (secretory canals absent).
   D. thyrsiflora (no secretory canals; some cells in center of pith sclerified; carbonized resin deposits in intercellular spaces).
   D. laevigata (no secretory canals; entire pith sclerified, more markedly so at periphery).
2. *D. linearis* (Fig. 16). Entire pith sclerified, not more so at periphery than at center; intercellular spaces small; no secretory canals; carbonized resin deposits not observed.
   Like *D. linearis:*
   D. Sherffiana, *D. reticulata* (carbonized resins in intercellular spaces).
3. *D. latifolia* (Fig. 17). Pith thin walled except at periphery, where it is prominently sclerified, and in the center, where nests of sclereids occur; the central sclereids are much narrower in diameter than other cells of the pith; intercellular spaces small; secretory canals absent; carbonized resin deposits in intercellular spaces of thin-walled area of pith. This pith type appears to be a marked specialization over the preceding types.
4. *D. Menziesii* (Fig. 18; Fig. 21, right). Pith highly lacunose, owing to large intercellular spaces; periphery consisting of small fiberlike sclereids adjacent to bundles; remainder of pith composed of large cells, both sclerified and unsclerified; no secretory canals; carbonized resins abundant in intercellular spaces. Figure 21 shows an early stage in the development of this pith, whereas pith from an old stem is shown in Figure 18. The progressive sclerification is evident, although some thin-walled cells remain in the pith shown in Figure 18.
   Like *D. Menziesii:*
   D. montana, *D. struthioloides*, *D. Hillebrandii* (virtually identical with *D. Menziesii*).
   D. arborea (fewer sclereids).

This type of pith would seem to represent a specialization over the condition indicated for *D. plantaginea*. An intermediate



FIGS. 15-20. Transections of pith. (15) *D. plantaginea*, × 75. (16) *D. linearis*, × 80. (17) *D. latifolia*, × 84. (18) *D. Menziesii*, × 78. (19) *Argyroxiphium Caliginii*, × 72. (20) *A. sandwichense;* packets of pith tracheids at right; groups of procambial cells below and left; × 90; inset shows bordered pits between two pith tracheids, × 870.

stage in specialization may be represented by *D. waialealae*.

5. *D. waialealae* (Fig. 22, right). Pith entirely thin walled, with large intercellular spaces; no secretory canals present; carbonized resin deposits in intercellular spaces.

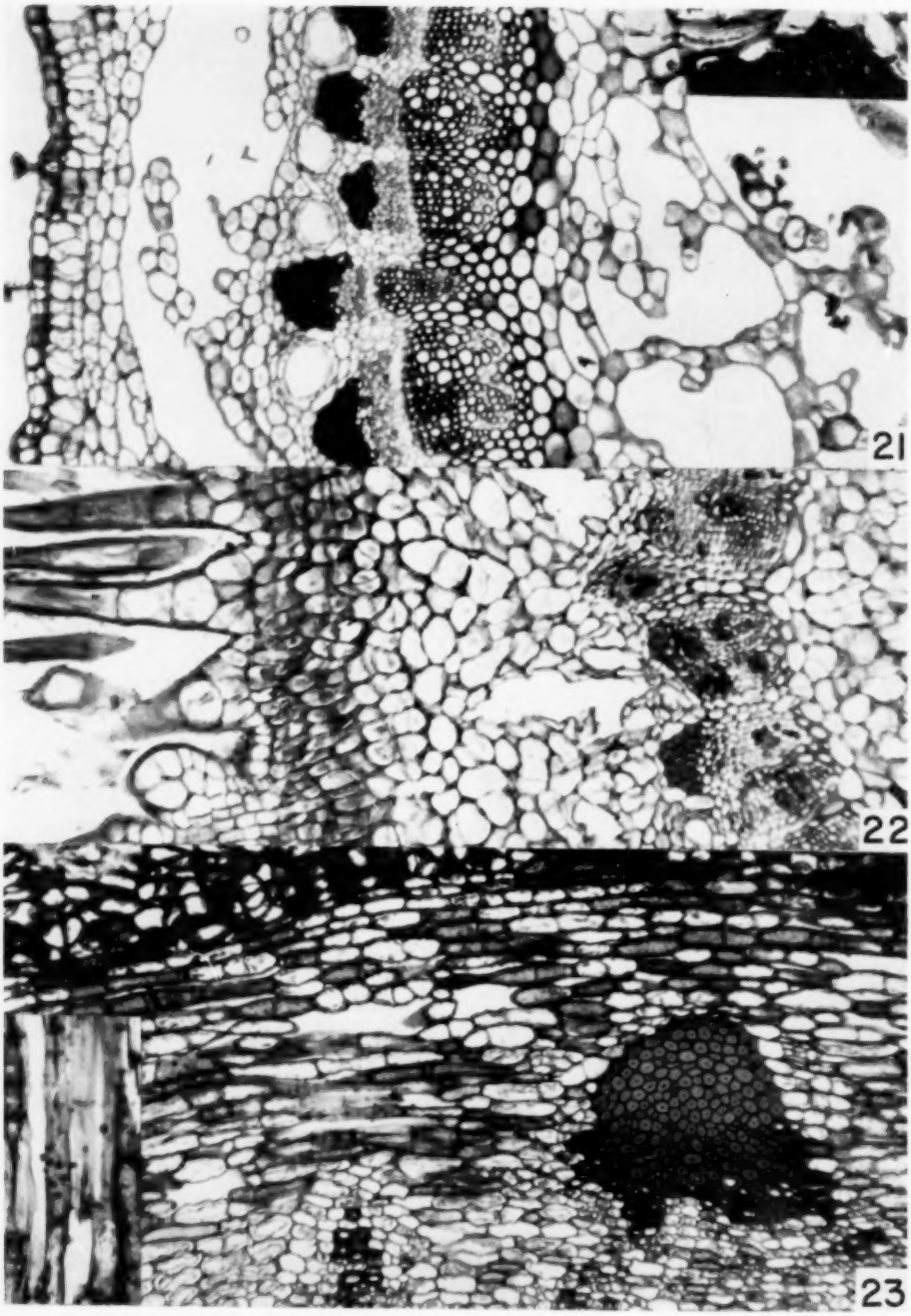
The pith of *Argyroxiphium Caliginii* (Fig. 19) is highly lacunose, and carbonized resin deposits are present. The inner margins of vascular bundles are clothed with a conspicuous zone of very thick-walled fibers. The remainder of the pith, however, remains thin walled and unlignified. An identical condition occurs in *A. Grayanum*. *Wilkesia* differs only in lacking carbonized resin deposits.

The pith of *Argyroxiphium sandwichense* (Fig. 20), however, shows a remarkable anomalous feature. Basically, pith in this species is identical with that of *A. Caliginii* in that it is lacunose and has fibrous caps on inner faces of the bundles. Into the large intercellular spaces of the cells of mature pith, however, new cells are proliferated by pre-existing pith cells. These new cells subdivide in various planes, often forming packets oriented in a particular direction. Most of these packets mature into sclerified cells (Fig. 20, right) although some of them (Fig. 20, left) apparently remain thin walled. Some of these sclerified cells, although somewhat elongate and fiberlike, have simple pits and should probably be termed sclereids. Others, as the inset in Figure 20 shows, have bordered pits and must therefore be termed tracheids. However, because Compositae do not have tracheids in the proper sense in their xylem, these tracheids are perhaps more nearly comparable to the "vascular tracheids" (i.e., degenerate vessels which lack perforation plates) which do occur in the secondary xylem of *A. sandwichense* (Carlquist, 1958). For the phenomenon described above, the term "pith tracheid" might be invented to accomodate their distinctive origin and mode of occurrence. The formation of these pith tracheids might be likened to the formation of tracheids in callus, such as those which occurred in the experiments of Wetmore and Sorokin (1955). The formation of nests of sclereids and pith tracheids in *A. sandwichense* pith, however, is apparently not related to preexisting vascular tissue, with which the pith tracheids are not in continuity. The formation of these nests is centripetal: the central portion of the pith was observed to contain only thin-walled cells, whereas such packets have matured into sclereids and tracheids near the periphery of the pith. A given nest may contain tracheids only, sclereids only, or a mixture of the two cell types. As in the experiments of Wetmore and Sorokin, no phloem could be detected in association with the pith tracheids.

Although the diversity of pith types in *Dubautia* is considerable, the pith of *Argyroxiphium* and *Wilkesia* does not match that of any given species of *Dubautia*. The presence of certain features, such as carbonized resins, is very similar, and pith of *Argyroxiphium* and *Wilkesia* can be considered to be within the range of the variation pattern of *Dubautia* pith.

Stem

The structure of the stem in respects other than nodal anatomy and pith anatomy is relatively uniform within *Dubautia*, *Argyroxiphium*, and *Wilkesia*, so that a small number of examples may be used, and variations may be described where they occur. In *Dubautia Menziesii* (Fig. 21), the vascular bundles develop prominent bundle caps of protophloem fibers. The layer of cells immediately exterior to the fibers is a well-marked endodermis (Fig. 21, inset) in which a Casparian strip may easily be demonstrated. The endodermis accompanies the bundle cap of a leaf trace in its departure from the vascular cylinder, although no endodermis occurs in leaf base or leaf. Although stem endodermis is uncommon in dicotyledons at large, it is frequent in Compositae, as the data of Metcalfe and Chalk (1950: 788) and Carlquist (1957*c*: 47) show. Numerous secretory canals are arranged adjacent to the vascular bundles.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Although the secretory canals appear at first glance to be arranged at random, examination of serial sections shows that they occur in pairs beside larger bundles which, farther up the stem, depart from the vascular cylinder as leaf traces. Cortical secretory canals, then, are initiated continuously with growth in length of the stem, because departure of secretory canals in association with leaf traces would result in their total absence in upper portions of a stem if new ones were not initiated. In *D. Menziesii*, cortical secretory canals continue into the leaf base for a short distance, although distal portions of the leaf lack them. In species which characteristically have such canals in the lamina, such as *D. Knudsenii* (Fig. 1), these canals continue from the stem into the leaf and either ramify or (particularly in the case of canals adaxial to veins) originate *de novo*. As the portion of a cleared leaf of *D. lonchophylla* in Figure 6 shows, these canals mainly parallel the larger longitudinally oriented veins. The cortex of *D. Menziesii* exterior to the secretory canals is highly lacunate. In the stem shown in Figure 21, cork formation is beginning. Periclinal divisions may be seen both in the epidermis and in the layer immediately beneath the epidermis. Cork formation, then is not restricted to a single layer of the stem. At extreme left in Figure 21, two degenerating biseriate glandular hairs may be seen.

The stem of *D. waialealae* (Fig. 22) illustrates several points of contrast. Only small lacunae are present in the cortex (gaps in that region in Fig. 22 probably resulted from the fact that a dried specimen was used for this preparation). Secretory canals are infrequent, although a small canal may be seen below the large bundle cap, lower right. Cork formation is not initiated in the epidermis, which is almost entirely involved in the formation of trichomes, but may be seen in the two or three cell layers below the epidermis. As in *D. Menziesii*, therefore, cork formation is not limited to a single layer. The hairs which thickly clothe the stem of *D. waialealae* are nonglandular and uniseriate in their upper portions. The multicellular nature of the trichome base results from elongation of epidermal cells subtending the hair. The trichome proper, therefore, may be termed uniseriate.

The differences between *D. Menziesii* and *D. waialealae* mentioned above are not great, and represent the extremes of variation observed in the genus. The majority of the species have moderately lacunate cortex, intermediate between these two types. Although secretory canals were found to be scarce or lacking in the stems of *D. waialealae* and *D. platyphylla* examined, they are present to some extent in the remaining species.

In the aspects of stem structure mentioned above, *Argyroxiphium* and *Wilkesia* are referable to exactly the same pattern. In *Argyroxiphium*, carbonized resin deposits, like those of the pith, occur in intercellular spaces in the cortex, as well as between fibers in bundle caps. *Argyroxiphium Caliginii* is the only species of its genus in which secretory canals are present in the leaves (Carlquist, 1957*d*): secretory canals accompanying leaf traces continue into the leaves. In other species, they terminate below the level at which leaf traces enter leaf bases. In *Wilkesia*, which also lacks foliar secretory canals, many of the leaf traces are not accompanied by secretory canals, although canals are abundant around the vascular cylinder proper. Secretory canals in *Wilkesia*, for the most part, terminate below separation of leaf traces from the cylinder.

Abundant cork formation from subepidermal layers is characteristic of *Argyroxiphium Caliginii* and *A. Grayanum*, whereas little cork occurs in the rosette species *A. sand-*

FIGS. 21–23. Transections of stems of *Dubautia*. (21) *D. Menziesii;* epidermis at left; × 98; inset shows endodermis with Casparian strip (line running through cells above fibers), × 350. (22) *D. waialealae*, × 115. (23) *D. platyphylla;* stem showing secondary growth; cork above, secondary phloem below; × 107; inset shows an area of lacunate cortex, enlarged, in which pectic warts are present on cell walls, × 218.

wichense and *A. virescens*. In *Wilkesia*, the layer beneath the epidermis is differentiated into a discrete hypodermis consisting of thick walled sclereids, and cork formation is initiated in a single layer immediately interior to the hypodermis.

The stems of both *Argyroxiphium* and *Wilkesia* lack endodermis demarcated by Casparian strips, although the formation of tangential sheets of cytoplasm in the layer of cells immediately exterior to bundle caps indicates that this layer of cells may be somewhat differentiated as an endodermis.

Biseriate glandular hairs with capitate multicellular heads are characteristically present on the stems of both *Argyroxiphium* and *Wilkesia*. These trichomes are of the same type as those illustrated by Carlquist (1957*d*) for inflorescence bracts of *Wilkesia* and *Argyroxiphium sandwichense*.

The similarities between stem structure of *Argyroxiphium* and *Wilkesia* and that of *Dubautia* are considerable, and are what one would expect if the three genera represent derivations from a common ancestry.

Secondary Growth

Aspects of secondary xylem structure in *Dubautia*, *Argyroxiphium*, and *Wilkesia* have been considered in an earlier paper (Carlquist, 1958). The stem of *D. platyphylla* (Fig. 23) demonstrates alterations in phloem and cortex structure as a result of secondary growth. Abundant cork development is evident, above. Formation of fibers in secondary phloem may be seen, below. The stem illustrated is young enough so that the cortex has not been ruptured, and characteristics of old cortical cells are shown. Cortical cells have experienced considerable tangential stretching. A particular feature of interest is the formation of pectic warts on the surfaces of cell walls which face intercellular spaces (Fig. 23, inset). These structures have been reported for cortical cells of Compositae only in *Wyethia ovata* (Carlquist, 1956). They do, however, occur on pith cells of *Argyroxiphium sandwichense* (Carlquist, 1957*d*).

Root

Roots of the genus *Dubautia* were not studied. In *Argyroxiphium* and *Wilkesia*, which the writer was able to grow from seed he collected in the Hawaiian Islands, anatomical studies were made. Adventitious roots of *A. Caliginii* were preserved in the field. Roots in these genera show typical dicot root structure. In *A. sandwichense*, roots varied from diarch to pentarch, depending on the diameter of the root. The primary root of the seedling, and all of the finer roots of a mature plant were found to be diarch. In the adventitious roots of *A. Caliginii*, which have a relatively larger diameter, five to seven xylem poles were observed. A variation of two to five xylem poles was observed in *Wilkesia*.

In roots of *A. sandwichense*, there are numerous small quadrangular "endodermal" secretory canals, of the type described by Tetley (1925) and Williams (1954). In the adventitious roots of *A. Caliginii*, a pair of somewhat larger secretory canals occurs exterior to each phloem strand. These secretory canals are similar to those figured by Carlquist (1957*c*: 116–119) for *Fitchia speciosa*. Small quadrangular secretory canals of the type found in *A. sandwichense* are characteristic of the roots of *Wilkesia*, although they may enlarge in size during secondary growth in the root.

In both *Argyroxiphium* and *Wilkesia* maturation of the central core of the root is characterized by fiber development more than vessel development. Conversion of some cortical parenchyma cells to sclereids was observed in roots of *Wilkesia* which showed secondary growth.

Secretory Canals: Summary

The details of secretory canal distribution in the vegetative parts of the plant have been detailed above. The fact that secretory canals are characteristic of all three genera is quite noteworthy, however. The mode of occurrence of these canals is highly reminiscent of the patterns in other Heliantheae, such as

Fitchia. The distribution of secretory canals in vegetative parts of *Dubautia*, *Argyroxiphium*, and *Wilkesia* follows very closely the diagram given by Carlquist (1957*c*: 58) for *F. speciosa*, differing only in those species which do not characteristically have secretory canals in pith, cortex, or leaves. The occurrence of secretory canals in inflorescence structures of *Dubautia*, *Argyroxiphium*, and *Wilkesia* will be considered in subsequent studies.

Trichomes: Summary

Although occurrence and types of trichomes have been mentioned above, the basic pattern underlying trichome occurrence needs to be stated. In the genera *Dubautia*, *Argyroxiphium*, and *Wilkesia*, two types of trichomes are present: uniseriate nonglandular and biseriate glandular. Examination of shoot apices indicates that these two types may be formed initially, but are variously matured or degenerate upon maturation of organs of the plant. In *Dubautia railliardioides*, for example, both uniseriate hairs and biseriate glandular trichomes with subdivided multicellular tips may be seen on young leaf primordia. On mature portions of the plant, both types of hairs are absent except for retention of uniseriate hairs in leaf axils. Thus, differences in indument of the mature plant are the result of elimination or retention of these two basic types. The leaves of *D. platyphylla* furnish an example of marked development of the biseriate hairs with subdivided pits, whereas leaves and stem of *D. waialealae* demonstrate conspicuously the uniseriate nonglandular hairs with no evidence, in the mature plant, of the biseriate type.

The precise nature and distribution of trichomes in Compositae is inadequately known. The occurrence of the capitate glandular hairs mentioned above, however, appears significant in connection with relations of the three genera to certain non-Hawaiian groups.

DISCUSSION

The importance of the data developed lies in the application of anatomical characters to taxonomy of the genera discussed, description of relationships among the three genera, and in determination of the relationships of these seemingly isolated genera. Within the genus *Dubautia*, characters of vegetative anatomy seem to offer good criteria for taxonomic decisions, although inflorescence anatomy cannot be overlooked.

The results of the present study, and one reported separately (Carlquist, 1958) indicate that Keck (1936: 24) is justified in uniting the species of *Railliardia* with *Dubautia*. No anatomical character, or combination of such characters, seems to support the division of the species into the two genera as they have been traditionally delineated. For example, *D. waialealae* (invariably treated as a *Dubautia*) seems closer in node and leaf anatomy to *D. Menziesii* (included under *Railliardia* by authors recognizing that genus) than to *Dubautia plantaginea* (type species of the genus) or its close relatives (*D. microcephala*, *D. railliardioides*).

Rather, the writer believes that a picture of species groups emerges, although these cannot yet be defined with sufficient precision to permit division of the genus into subgenera on the basis of the characters described here. Attention may be called, however, to certain alliances which seem quite certain:

(1) *D. Menziesii*, *D. arborea*, *D. Hillebrandii*, *D. montana*, and *D. struthioloides* agree in leaf, pith, and wood anatomy.

(2) The species with narrow strap-shaped leaves and wide leaf bases, *D. plantaginea*, *D. microcephala*, *D. railliardioides*, *D. paleata*, *D. magnifolia*, and *D. ternifolia*, seem close in leaf anatomy, presence of secretory canals in pith, and, to a certain extent, in nodal anatomy. *D. Knudsenii* appears close to this assemblage on the basis of its foliar secretory canals and its pith structure.

(3) A grouping of species including *D. ciliolata*, *D. lonchophylla*, *D. scabra*, *D. Sherffiana*, and *D. thyrsiflora* seems justifiable on the basis of near identity in leaf structure,

particularly in regard to the single secretory canal on the xylem face of veins.

Dubautia waialealae and *D. latifolia* show peculiarities of anatomy not closely matched by other species, and are probably rather isolated from whatever species each of them may most closely resemble. Each of these two species should probably form a "group" by itself. Inclusion of species other than those mentioned does not seem to be justified on the basis of present anatomical information.

The material for *Argyroxiphium* supports the interspecific relationships in that genus suggested earlier by the writer (1957*d*).

The suggestion of Keck (1936: 10) that *Dubautia*, *Argyroxiphium*, and *Wilkesia* must be considered a group within themselves could be defended on the basis of vegetative anatomy. The presence and distribution of trichome types, the patterns and nature of secretory canals, the lacunate character of the cortex, and the presence of carbonized resins in intercellular spaces are notable in this regard. In fact, the three genera could not be separated on the basis of some anatomical characters. Other structural features offer excellent criteria, however, and *Dubautia*, *Argyroxiphium*, and *Wilkesia* are amply distinct in respect to leaf and node anatomy.

Because there is little published information on anatomy of genera which are putatively related to these three genera, no comment can be made in this regard at present. The writer hopes to demonstrate, however, that characters described here are worthy of consideration in comparing these genera with such taxa as the American genera of Madinae, *Railliardella*, and certain Senecioneae.

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NOTES

A Note on Walford's Transformation

ROBERT H. RIFFENBURGH[1]

WALFORD[2] determines the asymptotic maximum of growth of an organism (or population) in the following manner. If size measure at successive ages N is plotted along an abscissa and size measure at successive ages N+1 along an ordinate, the points of intersection will form a linear function, say L_1, with slope less than unity. The line N = N+1, say L_2, will be the line of no growth; i.e. if size at age N+1 is the same as size at age N, no growth has occurred. The intersection of these two lines represents the desired asymptotic maximum for growth.

But L_1 is a line whose parameters are estimated from random variables and therefore which is itself a random variable. Often the slope of L_1 is so similar to that of L_2 that the random fluctuation of L_1 makes the desired point of intersection uncertain.

In general, if N+k, k a positive integer, is plotted against N, the same asymptotic maximum will occur, but L_1 will have slope sufficiently deviant from that of L_2 to permit confidence in the asymptotic maximum. k is chosen as the smallest integer assuring sufficient deviation.

[1] University of Hawaii and Pacific Oceanic Fishery Investigations. Manuscript received August 7, 1958.

[2] WALFORD, LIONEL A. A new graphic method of describing the growth of animals. *Biological Bulletin* 90(2): 141–147.

News Note

THE TENTH PACIFIC SCIENCE CONGRESS

The Pacific Science Congresses are held under the auspices of the Pacific Science Association. The Association was founded in 1920 by the holding of the First Pan-Pacific Scientific Conference in Honolulu, Hawaii.

A number of institutions and organizations, from 1900 on, planned and worked towards the systematic exploration of the Pacific, but the direct action resulting in this first Pacific science congress came from the Committee on Pacific Investigations of the U.S. National Research Council and its predecessor under the National Academy of Sciences, the Committee on Pacific Exploration.

The work of the Committee between 1916 and 1919 brought out the complexity of the problem, and a plan for a conference at which representative scientists from Australia, New Zealand, Java, China, Japan, Canada, continental U.S. and Hawaii, and the Philippines might be present.

The committee accepted the proposal that the conference might meet in Honolulu in 1920 under the auspices of the Pan-Pacific Union—a Hawaii organization devoted to developing friendly relations among the different nationalities of the Pacific. The program of the conference was arranged through

the Committee on Pacific Exploration of the National Research Council, and local arrangements were made by a committee appointed by the Governor of Hawaii and acting as a committee of the Pan-Pacific Union. The chairman of the congress was Professor Herbert E. Gregory, Director of Bishop Museum in Honolulu and Silliman Professor of Geology at Yale; the vice-chairman and secretary was Dr. Arthur L. Dean, President of the University of Hawaii.

The purpose of the congress was "to outline the scientific problems of the Pacific Ocean region and suggest methods for their solution. The conference undertook to take stock of our present knowledge of the Pacific area, its geography and geology, its plants and animals and the races of men which inhabit it, and proceeding from this comprehensive view to formulate the programs for future research."

In addition to defining the purpose of the congresses, and the scope of the program, the first congress set other important precedents. First, the congresses are nongovernmental, meaning that the scientists meet and discuss their problems as individuals and not as the representatives of their governments. Second, field trips are as much a part of the scientific program as the technical sessions. The first congress spent a week on the island of Hawaii, concentrating on the volcano Kilauea, which was obligingly active. The field trips are planned and led by the local scientists and are their opportunity to discuss in the field their particular problems.

Since that first congress in Honolulu, eight further Pacific Science Congresses have been held—Australia (1923), Japan (1926), Netherlands Indies (1929), Canada (1933), California, U.S.A. (1939), New Zealand (1949), Philippines (1953), and Thailand (1957). The Tenth Congress, returning to Hawaii, is planned for the last week of August and the first week of September, 1961.

Dr. Laurence H. Snyder will be president of the Tenth Pacific Science Congress. Dr. Snyder, who has accepted, is president of the University of Hawaii and a distinguished scholar in human genetics. He is immediate past president of the American Association for the Advancement of Science.

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CRAWFORD, DAVID L. 1920*a*. New or interesting Psyllidae of the Pacific Coast (Homop.). *Proc. Hawaii. Ent. Soc.* 4(1): 12–14.

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ROCK, JOSEPH F. 1916. The sandalwoods of Hawaii; a revision of the Hawaiian species of the genus *Santalum*. *J. Aust. Inst. Agric. Sci.* 12(3): 1–43, 13 pls.

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